THE DEVELOPMENT OF EVOLUTIONARY THOUGHT

Edited by

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Division of Natural Science

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Introduction

Evolution is the underlying principle that defines the biological sciences. This biological science course, unlike many others, begins with an investigation of evolutionary theory. Only after the theory has been defined and explored are the later discoveries that support the theory examined. In this sense the material in the beginning of this course is covered historically in the same sequence as the original discoveries were made. This is very different from most courses, which begin with the false assumption that we have always known all the "facts" we know today.

This reader includes five selections that deal with the historical development of the unifying theory in biology – **organic evolution**. The selections include information on the historical development of Darwin's theory of evolution by means of natural selection and the data that were used to support evolutionary thought. These readings allow students to trace the historical development of evolutionary theory and help students to better understand this important biological concept.

When most people think of science and the development of theories (models) they think of acquiring knowledge in a step-by-step process. A scientist builds a theory by carefully sorting through as much available evidence as possible, posing and testing hypotheses, and then finally advancing a theory that is supported by the evidence. This is the "data-model" loop that was introduced in the freshman course. However, more often than not theories are proposed before all the evidence necessary to support them is available. This was the case with evolutionary theory. Darwin brought together as much descriptive, empirical evidence supporting evolution as he could when he was formalizing his theory, yet much critical information was not available. How was genetic information passed from parent to offspring? What physical material was inherited? How could variation be maintained within populations? What evidence, other than the imperfect fossil record, was there to support slow gradual change of organisms over time? What was the exact age of the Earth? These represent just a few of the unsolved scientific problems Darwin faced as he prepared to publish his work in 1859.

For the modern student it is inconceivable that Darwin proposed his theory of evolution without knowing of the work in plant breeding done by Johann (Gregor) Mendel. Classical genetics as first proposed by Mendel is something that every student studies, often before they have even heard of Darwin. In an historical context Mendel had presented his findings in two lectures to the Natural History Society of Brünn (Brno) in 1865 and they were published in 1866, seven years after Darwin published the *Origin of Species* (Mayr, 1982). Although modern scientists would consider Mendel's research and publication exemplary, scientists at the time showed very little interest in Mendel's work. Mendel's paper was available to Darwin through the Linnaean Society of London, but there is no indication he ever was aware of this work. In fact, the significance of Mendel's work would not be fully recognized until 1900 and its relationship to Darwin's theory would not be solidified until the 1930s.

Also unavailable to Darwin was any knowledge of nucleic acids, which were first described by Friedrich Miescher in 1869. Miescher named this dark staining, phosphorus- rich material found in the nuclei of cells **nuclein.** Further analysis suggested that it was in fact very pure nucleic acid, which we now call deoxyribonucleic acid or DNA (Mayr, 1982). Miescher had no idea what the function of this substance was and it would be almost 100 years before DNA was universally accepted as the genetic material.

Further complicating the early acceptance of Darwin's theory was any understanding of how cells, especially reproductive cells, divide and pass on genetic material. Many scientists from the1840s through the1880s conducted significant work on cell division. The process of somatic cell division (**mitosis**) was well described by 1882 while **meiosis**, the division of reproductive cells leading to the production of gametes, was not fully described until a few years later (Mayr, 1982).

Darwin developed his theory of evolution by means of natural selection without knowing anything about Mendelian genetics, DNA or cell division. It is unlikely that a modern scientist would work in this way – developing a major, unifying theory without knowing the mechanisms by which it could occur. To many students it seems a bit backwards from the way we are taught science normally proceeds. Yet this is exactly what Darwin did. What Darwin did and how he did it was an extraordinary act of scientific genius. It should cause the modern student to examine more closely what Darwin's evidence was and how this evidence allowed him to suggest a culturally controversial theory without knowing the cellular mechanisms of inheritance.

The selections in this text are designed to provide greater insight into the discoveries associated with Darwinian evolution. Part I includes chapters from Daniel Boorstein's book, *The Discoverers* and provides an historical overview of the development of evolutionary theory. We will read this in two segments: 1) the chapters relating to pre-Darwinian ideas and 2) Darwin and the events that immediately followed the publication of the *Origin*. Part II includes chapters from the first edition of the *Origin of Species,* and the article by A.R. Wallace that stimulated Darwin to finally write his book. Part III is a chapter from a book by Loren Eiseley, which examines Mendel, his work, and how it relates to Darwinian evolution. Part IV is a chapter from a book on evolution by G.L. Stebbins, which summarizes the history of evolutionary theory and takes it beyond the **Modern Synthesis**. This last part is critical since many students have been taught that Darwin suggested the theory of evolution by natural selection in 1859 and from that date on evolution was the accepted theory. What is lost with this simplified interpretation are the differences that existed within the scientific community at the time of the publication of the *Origin*, and how the **Mendelians** and **Naturalists** had to come together in the 1930s -1940s to develop our modern view of evolution.

The text is by no means complete since papers dealing with Miescher and the early cytologists are not included. Students should use the readings to help them understand evolutionary theory and how it developed. Evolution is the unifying concept of the biological sciences. It permeates all aspects of science and our modern culture. Evolution is a scientific theory and it is a theory with a history. Complete understanding of modern evolutionary theory and its effect on human culture can only be achieved by examining its development. The readings in this text will help students develop their understanding of evolutionary theory

References

Mayr, E. 1982. *The Growth of Biological Thought*. The Belknap Press of Harvard University Press, Cambridge. 974 pp.

PEB

PART I

PRE-DARWINIAN VIEWS

Introduction

Boorstein, Daniel J.: *The Discoverers*, Chapters 54–59

Part I. Pre-Darwinian Views: Introduction

Evolution simply means change. One of the first things that anyone who examines the natural world will notice is that constant change is the only consistent feature observed. Seasons change with precise regularity. Organisms grow, develop, age and die. Longer-term change is possible to observe for those who are long-lived or who read the records of past observers. Aristotle characterized the realm of Earth as essentially different from the realm of the heavens, because change can and does happen here. Why, then, did the notion of change of life forms have such a difficult road to acceptance?

Daniel Boorstein, in this portion of his monumental work, *The Discoverers*, shows us the long and tortuous history of the idea of organic evolution: the understanding that change is not confined to individual organisms, but that whole populations, or species, of organisms can and do change over time. That one kind of organism can give rise to others different from ancestral forms, and that organisms and their environments interact to produce adaptation are notions that no educated person can today deny. In the mid-nineteenth century, however, very few educated persons would have considered these ideas worth their time, let alone their belief.

How did ideas about organic evolution develop? How did they gain acceptance? Like any idea that changes human thinking forever, the notion that species can change, and that environments can dictate which changes persist and which die out, has a long history. Like the similarly revolutionary idea that the Earth was not the center of the universe, ideas about biological change had to overcome significant opposition from established religion. More importantly, however, evolutionary ideas had to counter entrenched notions about the uniqueness of human beings, and our place in the biosphere.

Boorstein begins his history by looking at biodiversity, and early efforts to classify the astounding numbers of life forms catalogued by naturalists and travelers. Classification leads to thinking about the source of biodiversity, and Boorstein next shows how the definition of a species is the source of questions about whether life forms can vary or not. The names John Ray, Carolus Linnaeus, and the Comte de Buffon are important in this part of the historical treatment of evolutionary thought. All these men denied that species can change – yet all contributed greatly to the body of work that will eventually persuade Charles Darwin and Alfred Russel Wallace that evolutionary change is the cause of biodiversity. (And don't miss the wonderful description of Archbishop Ussher's calculations of the exact moment of the creation of the earth!)

Similarity in physical structure is one of the most compelling arguments for organic evolution. The work of Edward Tyson squarely addressed the thorny question of human origins, and made the idea that humans have an evolutionary history at least possible. The first real modern evolutionary theory, by Lamarck, suggested a mechanism for simpler forms to become more complex, and proposed that humans were a part of the evolutionary process. Last, Boorstein discusses the work of Darwin and Wallace, showing that their great contribution was built firmly on the foundation laid by such scientists as Ray, Linnaeus, Buffon, Tyson, and Lamarck.

Questions to consider:

1. How does classification lead to questions about the origin of biodiversity?
2. What was the Great Chain of Being? How is Lamarck's theory similar to the underlying ideas of the Great Chain?
3. What is meant by 'fixity of species'? Why was this idea such a difficult notion to overcome?
4. How does Buffon's idea about the interaction of organisms and their environment point towards evolutionary thought?
5. How do Darwin's and Wallace's experiences in the Pacific change their thinking about evolution?

SKSS

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Learning to Look

For fifteen hundred years the learned of Europe who wanted to know about nature relied on their "herbals" and their "bestiaries," textual authorities whose tyranny was quite like that of Galen over medicine, and whose poetic delights lured readers away from the outdoor world of plants and animals. Today when we read those guides we understand why medieval Europeans were so slow in learning to look. The pages of the illuminated herbals and bestiaries have never been excelled in charming whimsy or as miscellanies of home remedies.

These sources of medieval botany, the herbals, were the legacy of Dioscorides, the ancient Greek surgeon who had traveled about the Mediterranean with the armies of the emperor Nero. His *De materia medica* (c. 77) surveyed botany mainly as a kind of pharmacology. Physicians went about solemnly trying to match Dioscorides' description of plants he saw on the fringes of the warm Mediterranean with what they found in Germany, Switzerland, or Scotland. Like Galen, Dioscorides had studied Nature, but Dioscorides' disciples studied Dioscorides. He had vainly hoped that his readers would "not pay attention so much to the force of our words, as to the industry and experience that I have brought to bear on the matter." By an alphabetical arrangement earlier writers had separated "both the kinds and the operations of things that are closely related, so that thereby they come to be harder to remember." By contrast, he himself paid attention to where plants grew, to when and how they ought to be gathered, and even to the sorts of containers in which they should be stored. Like other classic authors, he produced few disciples and many exegetes. These treasured his words but forgot his example. He ceased to be a teacher as he became a text.

Yet to the practical-minded of the medieval centuries Dioscorides was delightfully appealing, for he did not distract his readers by theory or taxonomy. Written in Greek, Dioscorides' herbal arranged more than six hundred plants under everyday headings. Which should be sought out for oils, ointments, fats, or aromatics? Which would cure headaches or remove spots on the skin? What fruits or vegetables or roots were edible? What were local sources of spices? What plants were poisonous and what were their antidotes? What medicines could be made from plants?

Countless surviving manuscripts of "Dioscorides" attest his popularity throughout the Middle Ages. The more we read the texts, the less we are

puzzled by Dioscorides' popularity or by the surviving power of his nomenclature. For example, the first item among his "aromatics," in the translation (1655) by John Goodyer:

> Iris is soe named from the resemblance of the rainbow in heaven. . . . The rootes under are knotty, strong, of a sweet savour, which after cutting ought to be dryed in the shade, & soe (with a linnen thread put through them) to be layd vp. But ye best is that of Illyria & Macedonia. . . . The second is that of Lybia. . . . But all of them haue a warming, extenuating facultie, fitting against coughs, & extenuating grosse humors hard to get up. They purge thick humors & choler, being dranck in Hydromel to the quantity of seven dragms they are also causers of sleep & prouokers of tears & heale the torments of ye belly. But dranck with vinegar they help such as are bitten by venemous beasts, and the splenitick and such as are troubled with convulsion fitts, & such as are stiff with cold, & such as let fall their food.

The berry of the juniper, we learn, is "good for ye stomach, being good taken in drinck for the infirmities of the Thorax, Coughs, & inflations, tormina, & ye poysons of venemous beasts. It is also vreticall, whence it is good both for convulsions, & ruptures, & such as haue strangled wombes." The common radish "also breeds winde and heates, wellcome to the mouth, but not good for ye stomach, besydes it causeth belching and is vreticall. It is good for ye belly if one take it after meate, helping concoction ye more, but being eaten before, it doth suspend the meate; wherefore, it is good for such as desire to vomit to eate it before meate." The mandrake root can be prepared for anaesthesia "to such as shall be cut, or cauterized. . . . For they do not apprehend the pain because they are overborn with dead sleep. . . . But used too much they make men speechless."

A thousand years of "Dioscorides" manuscripts shows us what it meant to be at the mercy of copyists. With the advancing centuries, the illustrations move farther and farther away from nature. The copies of copies grew imaginary leaves for symmetry, enlarged roots and stems to fill out the rectangular page. Copyists' fancies became conventions.

Whimsical scribes took clues from the names as much as the properties of the plants, making botany a branch of philology. From the flowers of the Narcissus plant emerged tiny human figures, reminiscent of the unlucky youth who saw and loved his own image everywhere. The "Tree-of-life" was entwined by a serpent with a woman's head. The "Barnacle-tree" or "Goose Tree" bore shells that opened and hatched out the barnacle geese found in northern Scotland.

When the printing press first appeared in Europe, the most useful botanical information was still found in the ancient herbals as expanded and "improved" by generations of scribes. Printers with a heavy investment in

wood blocks or copperplates were then understandably reluctant to junk them simply because the pictures did not match the words of the text. Even scholars who might have been tempted to look at the plants themselves found it more convenient to compare manuscripts and gloss texts.

Printed herbals quickly became stock items. The *Liber de proprietatiibus rerum* (c. 1470), by an English monk who lived in the thirteenth century, went through twenty-five editions before the end of the fifteenth century. The vernacular opened avenues for facts from all Europe. But the herbal had obvious limits. Of every plant it always asked the same question: How can you amuse me, feed me, salve me, cure me?

In the late sixteenth century the holder of the chair in botany at the University of Bologna was still described as "Reader of Dioscorides." As each generation added its tidbits, seldom distinguished from the original, botanists and pharmacologists were mere commentators. The herbal was a catalogue of "simples," medicines each of which had only one constituent, usually from one plant.

The Italian physician Pierandrea Mattioli (1501–1577) offered the first translation of Dioscorides into a European vernacular. His commentaries in Italian (Venice, 1544) became a publishing phenomenon when it sold thirty thousand copies. Then by translating Dioscorides into Latin and adding synonyms for the plant names in several languages, he helped popularize the work across Europe. More than fifty editions in German, French, Czech, and other European languages made Mattioli's refurbished Dioscorides the ruler of botany for a continent.

What the herbals did for botany the bestiaries did for zoology. They, too, derived from a single ancient original, embroidered over centuries. And during the Middle Ages, they were exceeded in popularity only by the Bible. In our time the printed best seller speedily reaches across space but only seldom reaches out into the generations. In the age of the manuscript the power of a single classic author was deathless. The Empire of the Learned was ruled by an oligarchy of a few chameleon "authors." Classic names were made to serve later generations by countless latent revisions, and the original author became a phantom. The hand of the scribe overruled the author.

The original of the bestiaries took its name from a Greek, Physiologus ("Naturalist"), about whom we know very little. His work, probably written before the mid-second century, appears to have been divided into forty-eight sections, each linked to a text from the Bible. A few facts, embellished by abundant theology, morality, folklore, myth, rumor, and fable, provided zoology for generations. By the fifth century there were translations, besides the Latin, into Armenian, Arabic, and Ethiopian. Later it was among the earliest works translated into the European vernaculars, including Old High

German, Anglo-Saxon, Old English, Middle English, Old French, Provençal, and Icelandic.

The Greek version included some forty animals in a delectable potpourri. Naturally, the lion, king of the beasts, comes first, and with three salient facts: he uses his tail to rub out his footprints so hunters cannot follow him; he sleeps with his eyes open; and the newborn cub remains dead for three days until the father lion breathes life into it. So, too, the body of Christ was dead, yet like the newborn lion, He remained awake and ready for Resurrection on the third day.

The remaining animals—lizard, night raven, phoenix, hoopoe, and thirty-odd others—carry a heavy baggage of morals. None is more vivid than the "ant-lion," offspring of the unnatural union of a lion and an ant, who is doomed to starve because the nature of the ant will not permit it to eat meat, and the nature of the lion keeps it from eating plants. So, too, none can survive who try to serve both God and the Devil.

Many "translations" were in verse, because bad verse was more memorizable than good prose. Compounding from Physiologus' work, Pliny and others pioneered with bestiaries in the new European vernaculars. For example, the *Bestiare d'amour* of Richard de Fournival delighted readers at court with the verses of a nobleman urging his lady love to imitate the turtle dove. But, instead, she imitates the aspis snake and covers her ears so as not to be seduced by his honeyed words.

"Ask now the beasts," urged Job in a favorite passage of the bestiaries, "and they shall teach thee; and the fowls of the air, and they shall tell thee: Or speak to the earth, and it shall teach thee: and the fishes of the sea shall declare unto thee." Since God himself had named his creatures, the name of anything was a clue to its meaning. Birds, we are told, are called A-*ves* "because they do not follow straight roads *(visas),* but stray through any byway." "*Ursus* the Bear, connected with the word '*Orsus*' (a beginning), is said to get her name because she sculptures her brood with her mouth *(ore).*"

If we see an uplifting symbolism of divine symmetry, Saint Augustine himself had declared, we should not worry whether a creature really exists. There must of course be a sea horse because there is a horse on land, just as the serpent on land suggests an eel in the sea. And because there is a Leviathan (a female monster in the sea), there must be a Behemoth (a male monster on the land).

Myths, unlike facts, were uncorrectable. Who could persuade us to abandon Narcissus, the Phoenix, or the Sirens? Modern authors—Lewis Carroll, E. B. White, Thurber, Chesterton, Belloc, and Borges—have kept legends of the animate world alive with their own flights of wit and fancy.

In the herbals and the bestiaries the author and the illustrator were not only different people, they were sometimes separated by centuries. The earliest surviving copy of *De materia medica,* made about A.D. 512, four centuries after Dioscorides' death, offered illustrations copied from those by Krateuas, who had died a century before Dioscorides was born. Commonly scribes wrote the text, leaving space for the illustrator to fill in later, but sometimes the tasks were done in reverse order. Often illuminators could not read the language of the text, and sometimes they could not read at all. Occasionally the master named in the margins the miniature to be copied. Over the centuries different illustrations were used for the same text, and vice versa.

Pliny himself (A.D. 23–79) had noted the difficulties:

> Some Greek writers . . . adopted a very attractive method of description, . . . It was their plan to delineate the various plants in colours, and then to add in writing a description of the properties which they possessed. Pictures, however, are very apt to mislead, where such a number of tints is required for the imitation of nature with any success; in addition to which, the diversity of copyists from the original paintings, and their comparative degrees of skill, add very considerably to the chances of losing the necessary degree of resemblance to the originals. . . .
>
> Hence it is that other writers have confined themselves to a verbal description of the plants; indeed some of them have not so much as described them even, but have contented themselves for the most part with a bare recital of their names, considering it sufficient if they pointed out their virtues and properties to such as might feel inclined to make further inquiries into the subject.

Only a rare few who combined in themselves the talents of both naturalist and artist could transform miscellaneous objects into specimens (from Latin *specere,* "to look at" or "to see"), items not merely written about but shown. The contrast between the schematic designs of the herbals and the true-to-life botanical drawings done about 1500 by Leonardo da Vinci or Dürer is startling. Leonardo himself recalled having made "many flowers drawn from life," and from his renderings of a bramble, a wood anemone, and a marsh marigold modern botanists can unmistakably identify each of the species. Dürer's vivid meadow turf—the random cluster of a dozen different grasses—seen from sod level is said to be the first precise ecological study in botany.

In that Age of Discovery when novelties of all sorts were flooding Europe from distant New Worlds, botanists became discoverers in their own backyards. In one region of Europe, clusters of artists and scientists began collaborating in a variety of new ways, and illustrators lured naturalists out of libraries into the field. As early as 1485 Peter Schöffer, who began as assistant to Gutenberg's associate and successor Johann Fust, had printed

an herbal in Mainz, and other popular variations on Dioscorides followed. The modern era in botany was opened by *Living Portraits of Plants* (*Herbarum Vivae Eicones,* 1530)—the joint product of a physician, Otto Brunfels (1489–1534), and an artist, Hans Weiditz—at long last an herbal with illustrations drawn from nature. Brunfels, in the familiar pattern, was destined for the priesthood but turned to medicine, prepared a scholarly medical bibliography, then a new edition of Dioscorides adapted to his own neighborhood. He could not resist including the beautiful pasqueflower, but since it had not been authenticated by Dioscorides and so had no Latin name, he condescendingly labeled it, and others not found in the sacred text, naked orphans *(herbae nudae).* The text was still substantially traditional. But the artist proved bolder than the scholar, and as the title of the book announced, Hans Weiditz had drawn directly from nature. What Leonardo and Michelangelo were doing for the human figure, Weiditz did now for the botanical figure. Of course, faithfulness to the observed specimen would not always please. If it had withered leaves, broken stems, truncated roots, or had been eaten away by insects, just so he drew them.

The courage to look and to draw what was really there was slow in coming. For in this last epoch of herbals the printing press still perpetuated the power of ancient texts. Just as Luther had attempted to reform Christianity by returning to the Bible, so Leonhart Fuchs (1501–1566) urged physicians to return from later commentaries to the original text of Galen, and he produced his own edition (Basel, 1538). Raised in the Swabian Alps, as a boy he would walk through the countryside with his grandfather, who told him the names of flowers. At the university he was taught by the humanist Johann Reuchlin (1455–1522), he read Luther, and became professor of medicine. Then in his herbal, *De Historia Stirpium* (1542; German translation, 1543), he paid heavy tribute in its text to Dioscorides and other ancients. But he boldly departed from ancient visual models. To provide the brilliant illustrations, he had organized a team of artists—one who drew the plants from nature, another who copied the drawings onto the wood blocks, and a third who carved the blocks. The front of the book showed a portrait of each of these "mere" craftsmen.

Far beyond the canon of Dioscorides, the illustrations included woodcuts of four hundred native German plants and one hundred foreign plants. "Each of which," Fuchs' Preface explained, "is positively delineated according to the features and likeness of the living plants . . . and, moreover, we have devoted the greatest diligence to secure that every plant should be depicted with its own roots, stalks, leaves, flowers, seeds and fruits. . . . we have purposely and deliberately avoided the obliteration of the natural form of the plants by shadows, and other less necessary things, by which the delineators sometimes try to win artistic glory." Fuchs' enthusiasm shone

through, for "there is nothing in this life pleasanter and more delightful than to wander over woods, mountains, plains, garlanded and adorned with flowerlets and plants of various sorts, and most elegant to boot, and to gaze intently upon them." He still arranged items in alphabetical order.

Fuchs' herbal, which now actually deserved to be called a work of botany, set the standard of plant illustration for modern times, later exciting the admiration of William Morris and John Ruskin. From the New World voyages Fuchs harvested some American plants, notably Indian corn, and posthumously he became the eponym of one of the most beautiful American tropical plants, the fuchsia.

In some ways Hieronymus Bock (1498–1554), the third German father of botany, was even more remarkable. Having first tried to identify the Greek and Latin names with the plants in his part of Germany, he went on, and in his *Neu Kreütterbuch* (1539) he freely described all the plants seen in his neighborhood, and set himself the still novel task of describing local plants in the local language.

All these German fathers of botany were active Lutherans at a time when defying the Church of Rome certainly cost you your professorship, and possibly your life. Their botanical dogma, like the Lutheran dogma, was ambivalent. While they went back to a purified text of their sacred Dioscorides, they also put botanical learning, as Lutherans had put the Bible, into the language of the marketplace.

Reaching far beyond the familiar charms of the German countryside, sixteenth-century Europe was delighted by reports of exotic plants and animals from "the Indies," East and West. New World "facts" did not automatically increase the stock of new knowledge. For sailors, as Shakespeare recounted, enjoyed sensationalizing their experiences—with tales of men whose heads grew beneath their shoulders, or who had no heads, or those like the Patagonians who had a single large foot, or the Labradoreans who bore tails. What followed, the historian Richard Lewinsohn reminds us, was a "Rebirth of Superstition." Out of the Americas, whole new orders of monstrous races and fantastic animals were created. Since it is almost as hard to think up a new animal as to discover one, flimsy facts were grafted onto the familiar creatures of myth and folklore.

The Age of Discovery brought a renaissance of fable. Sea serpents five hundred feet long flourished as never before. Mermen and mermaids were now described in unprecedented detail—tall males with deep-set eyes and long-haired females—hungry for their meal of Negroes or Indians, but eating only the bodily protuberances, the eyes, noses, fingers, toes, and sexual organs. Columbus himself reported his encounter with three Sirens. And, of course, the unicorn's horn was so magically therapeutic that, at the

marriage of Catherine de' Medici to the French dauphin, Pope Clement VII himself made the princely gift of one to King Francis I. Doubtful legends were now authenticated by the testimony of Jesuit missionaries, substantial sugar-planters, and sober sea captains. To the figments of medieval fantasy were added the real creatures from every new voyage to the Americas. Those who could not read a Latin text could enjoy the copious printed illustrations.

These opportunities inspired a new generation of encyclopedists of nature. The most remarkable of them, Konrad Gesner (1516–1565), had a genius for grafting the new onto the old. Prodigiously learned in several languages, Gesner was torn between what he had read and what he saw. He was born into a poor Zurich family in 1516, educated himself as a vagrant scholar, and, when he was only twenty, wrote a Greek-Latin dictionary. In the next thirty years he turned out seventy volumes on every conceivable subject. His monumental *Bibliotheca Universalis* (4 vols., 1545–1555) aimed to provide a catalogue of *all* writings that had ever existed in Latin, Greek, and Hebrew. Gesner listed eighteen hundred authors and titles of their works in manuscript and in print, with summaries of their content. Thus he earned his title as the Father of Bibliography. What cartography was to explorers on land and sea, bibliography would be to libraries.

In the library of the Fuggers he came upon an encyclopedic Greek manuscript of the second century which inspired him to become a modern Pliny. Finally his *Historia Animalium,* following Aristotle's arrangement, supplied everything known, speculated, imagined, or reported about all known animals. Like Pliny, he provided an omnium-gatherum, but now added the miscellany that had accumulated in the intervening millennium and a half. A shade more critical than Pliny, he still did not deflate tall tales, as when he showed a sea serpent three hundred feet long. But he circumstantially described whale hunting and offered the first known picture of a whale being skinned for blubber. The enduring influence of Gesner's work came from his feeling for folklore and his power to depict fact and fantasy with equally persuasive vividness.

Within a century the English reader had ready access to Gesner's popular encyclopedia in Edward Topsell's translation, which he called the *History of Four-Footed Beasts, Serpents, and Insects* (1658). There we learn of the Gorgon:

> there ariseth a question, whether the poyson which he sendeth forth, proceed from his breath, or from his eyes. Whereupon it is more probable, that like the Cockatrice he killeth by seeing, then by the breath of his mouth, which is not competible to any other Beasts in the world. . . . By the consideration of this Beast there appeareth one manifest argument of the Creators divine wisdom and Provi-

> dence, who hath turned the eyes of this beast downward to the earth, as it were thereby burying his poyson from the hurt of man: and shadowing them with rough, long, and strong hair, that their poysoned beams should not reflect upwards, untill the Beast were provoked by fear or danger. . . .

After the unassailable testimony of the Ninety-second Psalm, he describes how unicorns are sacred because they "reverence Virgins and young Maids, and that many times at the sight of them they grow tame, and come and sleep beside them. . . . for which occasion the Indian and Aethiopian Hunters use this strategem to take the beast. They take a goodly strong and beautiful young man, whom they dress in the apparel of a woman, besetting him with divers odoriferous flowers and spices."

Despite the fantasies of his text, Gesner's thousand woodcuts helped set a new direction in biology. Like the German botanic fathers, Gesner collaborated with artists and provided the most accurate drawing yet of all sorts of creatures, from "the Vulgar Little Mouse," to the Satyre, the Sphinx, the Cat, the Mole, and the Elephant. His illustration for the Rhinoceros, "the second wonder in nature . . . as the Elephant was the first wonder," was made by Dürer. These incunabula of biological illustration began to liberate readers from herbals and bestiaries.

Gesner's work, reprinted, translated, and abridged, dominated zoology after Aristotle until the pathbreaking modern surveys of Ray and Linnaeus, which were not illustrated. His unpublished notes became the basis in the next century of the first comprehensive treatise on insects. For his *Opera Botanica* he collected nearly a thousand drawings, many by himself, but his great work on plants, his first love, he never completed.

He never quite freed himself of his philological obsession. His 158-page book, *Mithridates, or observations on the differences of languages, which have been or are in use among various nations of the whole world* (1555), tried to do for languages what he was already doing for animals and plants. "All" the world's one hundred and thirty languages were described and compared in Gesner's translations of the Lord's Prayer. Incidentally, for the first time, he provided a vocabulary of the Gypsy language.

Gesner found a more characteristically Swiss way to discover nature when he advertised the adventure of exploring the high mountains, which, as we have seen, had so long been a scene of awe and terror. Renaissance Europe saw a brief, if premature, flash of the mountain-adventuring spirit. Petrarch (1304–1374) had led the way near Avignon in 1336 with his ascent of Mt. Ventoux. At the summit he read from the copy of Saint Augustine's *Confessions* that he took from his pocket the caution that people may "go to admire the high mountains and the immensity of the ocean and the course

of the heaven . . . and neglect themselves." Leonardo da Vinci, with the eyes of an artist-naturalist, explored Monte Bo in 1511. The Swiss Reformer and humanist Joachim Vadianus (1484–1551), friend of Luther and champion of Zwingli, reached the summit of the Gnepfstein near Lucerne in 1518.

But Gesner was the first European to publish a paean to mountaineering. After his ascent of Mt. Pilatus near Lucerne in 1555, he produced his little classic.

> If you wish to extend your field of vision, cast your glance round about, and gaze off far and wide at everything. There is no lack of lookouts and crags on which you may seem to yourself to be already living with your head in the clouds. If on the other hand you should prefer to contract your vision, you will gaze on meadows and verdant forests, or even enter them; or to narrow it still more, you will examine dim valleys, shadowy rocks and darksome caverns. . . . In truth nowhere else is such great variety found within such small compass as in the mountains; in which . . . one may in a single day behold and enter upon the four seasons of the year, summer, autumn, spring and winter. In addition, from the highest ridges of mountains the whole dome of our sky will lie boldly open to your gaze, and the rising and setting of the constellations you will easily behold without any hindrance; while you will observe the sun setting far later and likewise rising earlier.

Primitive fears were so hard to overcome that two centuries separated Gesner's sallies from the true beginnings of modern mountaineering. Mont Blanc (15,771 ft.), the highest mountain in Europe outside the Caucasus, was not scaled until 1786—by someone who wanted to claim the money-reward offered by a patrician Swiss geologist, Horace-Bénédict de Saussure (1740–1799), twenty-five years before.

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The Invention of Species

So long as naturalists arranged plants and animals in alphabetic order, the study of nature was doomed to remain bookish and provincial. That order of items would depend, of course, on the language you were reading. The Latin version of Gesner's authoritative encyclopedia opened with *Alces,* the

moose, but when translated into German the book began with *Affe,* the ape, while in Topsell's *History of Four-Footed Beasts,* Chapter One described "The Antalope."

Naturalists needed a precise way of naming plants and animals across the language barriers. Even before that, they had to have a common understanding of what they meant by a "kind" of plant or animal. What were nature's units? When pioneer naturalists formulated the concept of "species" they would provide a useful vocabulary for cataloguing the whole creation. In the long run, the new mode of description would open many unanswerable questions. Meanwhile it enlarged the vista of nature's variety. And the quest for a "natural" way of classifying the creation would produce some of the great intellectual adventures of modern time.

In the older popular encyclopedias, such as Topsell's *History of Four-Footed Beasts,* an impenetrable fog enveloped the boundaries between the kinds of animals. Aristotle had described only some five hundred.

A difficulty that we have forgotten lay in the widespread belief in spontaneous generation. Aristotle had written that flies, worms, and other small animals originated spontaneously from putrefying matter. In the seventeenth century the eminent Flemish physician and physiologist Jan Baptista van Helmont (1577–1644?) said that he had seen rats originate in bran and old rags. If animals could arise spontaneously, then it was not feasible to define a species as a creature that reproduced or was reproduced by its own kind.

Only gradually and reluctantly did European naturalists give up this idea. Aristotle's contempt for "lowly" vermin and insects, as we have seen, had been based on his notion that they did not have the differentiated organs found in "higher" animals. Francesco Redi (1626–1697?), a Florentine member of the Accademia del Cimento, who had discovered how snakes produced their venom, was interested in other "lowly" creatures, including insects. After Leeuwenhoek's microscope showed how complex were tiny animals, it was easier for naturalists like his fellow Dutch biologist Swammerdam to argue that these animalcules did not arise by spontaneous generation, but had reproductive organs. And Redi described the parts of insects that produced their eggs. "Flesh and plants and other things . . . putrefiable play no other part, nor have any other function in the generation of insects," he suggested in 1688, "than to prepare a suitable place or nest into which, at the time of procreation, the worm or eggs or other seed of worms are brought and hatched by the animals; and in this nest the worms, as soon as they are born, find sufficient food on which to nourish themselves excellently." Redi had covered putrefying meat with cloth or put it in closed flasks, and so demonstrated that if flies could not reach the meat to lay their eggs no maggots would appear. But he still found some other cases where

he suspected spontaneous generation, and the question was to remain alive for two more centuries.

The idea of species would be usefully defined, developed, and applied by biologists long before the notion of spontaneous generation was laid to rest. And the issue was unresolved because it had theological overtones. Radical scientists found the idea of spontaneous generation useful for their natural-scientific explanation of the origin of life, which would have made God's role in the Creation superfluous. Louis Pasteur (1822–1895), the ambitious and hardheaded son of a French tanner, a faithful conservative Catholic and a brilliant experimentalist, saw the matter differently. To him an orderly concept of species was necessary for God's creative work in the Beginning. After acrimonious debate, his simple experiments with fermentation proved the prevalence of microorganisms in airborne dust, and showed that heating and the exclusion of airborne particles would prevent the appearance of vegetation. The successful application of his ideas to "pasteurizing" milk and improving production of beer and wine helped clinch the arguments against spontaneous generation.

When we think of the difficulty of devising a comprehensive system for classifying the whole creation, we are not surprised that the writers of herbals and bestiaries arranged items either alphabetically or according to their human uses. Since the differences between animals are usually more conspicuous than those between plants, the first efforts at general classification were made for animals. Medieval writers derived their first scheme from Aristotle, who had divided the animals with red blood from all others, which he called bloodless. The "blooded" animals were then subdivided according to modes of reproduction (live-bearing or egg-laying) and according to habitat, and the others were subdivided by general structure (weak-shelled, hard-shelled, insects, etc.). Aristotle himself actually used a concept of genus from Greek *genos,* or family; and species from *eidos,* or form, which he seems to have derived from Plato. But for him neither "genus" nor "species" had the sharp definition that they would acquire in modern times. His "genus," or family, designated all groupings larger than the species. Aristotle's rough scheme served European naturalists tolerably well during the Middle Ages, when relatively few novel plants and animals were coming to their notice. They devoted themselves to matching the plants and animals of their region with those described in the ancient texts.

Then in the Age of Discovery countless novelties poured into the European consciousness. How should these be arranged? How could you know whether a particular plant or animal really was new?

Specimens, books, travelers' tales, and newly vivid drawings from nature appeared in profusion and confusion. Encyclopedias like Gesner's piled fancy onto fact. Curiosities from everywhere were jumbled together. For

example, a handsomely illustrated volume on the plants and animals of Brazil by the pioneer German illustrator Georg Markgraf (1610–1644) was garbled with William Pies' work on the natural history of the East Indies. Readers were delighted by such potpourris. The word "herbarium" came into use to describe the collection of neatly pressed dried plants piling up in the libraries of noblemen and naturalists. Where should each specimen be placed? How should each one be labeled, organized, or retrieved?

To find a "system" in nature, naturalists first would have to find or make units for their system. This purpose was served by the concept of "species." In the hundred years between the mid-seventeenth century and mid-eighteenth century, more progress was made in cataloguing the varieties of nature than had been accomplished in the whole preceding millennium.

Two great systematizers—Ray and Linnaeus—would accomplish for all plants and animals what Mercator and his fellows did for the planet's whole surface. Just as the map-makers of the [illegible]th started from the self-evident boundaries of land and sea, mountains and deserts, the naturalists, too, found self-evident units among plants and animals. Still, as we have seen, even for the earth's surface it was necessary to invent the artificial boundaries of latitude and longitude so others could find their way and all could share the increasing knowledge. Similarly, these naturalists had to supply units that could help others everywhere find their bearings in nature's prolific jungle. Like the "atoms" of the physical system, these "species" would eventually be opened and dissolved, but meanwhile they provided an essential and convenient vocabulary. By the late twentieth century, "species" had become so familiar and so useful that it seemed essential to our thinking about plants and animals, somehow self-evident in the fabric of nature.

In its very beginning the notion of "species" was a labored and controversial product. It was fortunate for the future of biology that John Ray (1627?–1705) invented his definition of species just when he did. Unlike earlier schemes, his applied both to plants and animals and made it possible for his great successor to devise a system for cataloguing the whole creation. At Trinity College, Cambridge, Ray studied classics, theology, and the natural sciences (B.A., 1648), then as a fellow of the college he lectured to undergraduates on Greek and mathematics. Had it not been for the Act of Uniformity, passed by Charles II's Parliament in 1662, he might have remained only another fellow on the college rolls. That Act required clergy, college fellows, and schoolmasters to take an oath accepting everything in the Book of Common Prayer, but Ray would have none of it. Rather than compromise his conscience, he gave up his fellowship.

Another lucky coincidence was Ray's meeting with a wealthy younger

member of his college, Francis Willughby (1635–1672), who would make it possible for Ray to spend his life as a private, independent scholar. After a boyhood illness, Ray had formed the habit of country walks, and Ray and Willughby became boon companions, walking the Cambridge countryside together. Ray pursued his scientific interests by describing all the plants he saw, and then went on to survey the plants elsewhere in England. He produced a catalogue of English plants in 1670, incidentally noting variations in proverbs and word usage in different parts of the country, combining the taxonomy of words with that of all other living things. Ray and Willughby together toured the Low Countries, Germany, Italy, Sicily, Spain, and Switzerland, along the way noting the plants. En route they formed a grandiose plan, the sort of youthful pact often made and seldom fulfilled. They would collaborate on a comprehensive *systema naturae*—a description of the whole scheme of nature based on their own observations. Ray would cover the plants, Willughby the animals. This ambitious project was well along when Willughby died in 1672 at the age of thirty-seven.

Meanwhile Ray's letters to Oldenburg had so impressed the Royal Society that not only did they elect him a Fellow but when Oldenburg died in 1677 they offered him the powerful position of Secretary of the Society. But Ray refused, for in his will Willughby had left Ray an annual stipend, and instead of becoming a middleman for other scientists, he preferred to remain an independent naturalist. He moved into Willughby's Middleton Manor, where he revised Willughby's manuscripts and published two substantial treatises, one on birds, and another on fishes, both under Willughby's name.

Then under his own name Ray produced his epoch-making works on plants. His brief *Methodus Plantarum* (1682) offered the first feasible definition of "species," and his *Historia Plantarum* (3 vols., 1686–1704) provided a systematic description of all plants known to Europe at the time. Although Ray started from Aristotle, he went on to develop a more satisfactory arrangement, grouping plants not merely by some single feature like their seed, but according to their whole structure. Following the old axiom that "Nature does not proceed by leaps" *(Natura non facit saltus),* Ray sought out "middle terms," forms that stood between others to fill out the spectrum of the creation. He also improved on Aristotle's general classification of animals, appealing again to affinities of forms. This arrangement has proved useful ever since. Ray went on to survey quadrupeds and serpents, and made the pioneer comprehensive description of insects.

Before Ray's death the grandiose youthful Ray-Willughby scheme for a survey of nature's system based on firsthand observation was near completion. Unlike the alphabetical compendia of Gesner and his predecessors, Ray's work omitted the cherished mythical creatures. Having rid himself

of this baggage, and having denied spontaneous generation, he was in a position to define the units of natural life for succeeding generations of naturalists.

Ray's great achievement was his formulation or, more precisely, his invention, of the modern concept of "species." What Newton did for students of physics with his concepts of gravitation and momentum, Ray did for students of nature. He gave them a handle on a system. Like many other world-shaping ideas, his notion was wonderfully simple. Precisely how he came upon it we do not know. But his bold insight and his emphasis must have been stirred by his wide-reaching personal observations in the field. For Ray, finally, the sight of so many different *specimens* suggested the convenience of a concept of *species* (which also derives from the Latin *specere*, "to look at" or "to see.") Unlike his predecessors, he found a system of classification that would serve for both animals and plants.

Others, including Aristotle, had approached the problem by first dividing organisms into large, presumably self-evident, groups, and then subdividing these into smaller and smaller groups. Ray, on the contrary, began with an awe for the uniqueness of individuals and the wonderful variety of "species." As he explained in the Preface to his *Methodus Plantarum*:

> The number and variety of plants inevitably produce a sense of confusion in the mind of the student: but nothing is more helpful to clear understanding, prompt recognition and sound memory than a well-ordered arrangement into classes, primary and subordinate. A Method seemed to me useful to botanists, especially beginners; I promised long ago to produce and publish one, and have now done so at the request of some friends. But I would not have my readers expect something perfect or complete; something which would divide all plants so exactly as to include every species without leaving any in positions anomalous or peculiar; something which would so define each genus by its own characteristics that no species be left, so to speak, homeless or be found common to many genera. Nature does not permit anything of the sort. Nature, as the saying goes, makes no jumps and passes from extreme to extreme only through a mean. She always produces species intermediate between higher and lower types, species of doubtful classification linking one type with another and having something in common with both—as for example the so-called zoophytes between plants and animals.
>
> In any case I dare not promise even so perfect a Method as nature permits—that is not the task of one man or of one age—but only such as I can accomplish in my present circumstances; and these are not too favourable. I have not myself seen or described all the species of plants now known.

For Ray, a species of plants, for example, was a name for *a set of individuals who give rise through reproduction to new individuals similar to themselves.* Among animals the same definition would apply. Bulls and cows were

members of the same species because when they mated they produced a creature like themselves.

Ray believed that, as a general rule, each species was fixed and did not vary throughout the generations. "Forms which are different in species always retain their specific natures, and one species does not grow from the seed of another species." As time passed and he studied more and more specimens he saw that minor mutations might be possible. "Although this mark of unity of species is fairly constant," he concluded, "yet it is not invariable and infallible."

Biologists after Darwin uncharitably criticized Ray for his belief in the fixity of species, a proposition that his successor Linnaeus embraced with even more enthusiasm. But in his own day, Ray's insistence on that fixity and continuity of species was a giant step forward. It would make possible an internationally usable catalogue of the whole natural world. His insistence on the power of each species to continue to generate like organisms helped Ray dispose of much baggage that had burdened biologists from antiquity through the age of Gesner. He helped rid scientific literature of the mythical creatures attested in belles lettres and folklore who always propagated more mythical creatures. And he put an indelible question mark beside all "spontaneously generating" creatures. Just as the post-Newtonian world was governed by the laws of physical gravitation, at last biologists were being led into a world governed by the laws of biological generation.

Lyell and other pioneers of geology would introduce uniformitarianism into the history of the earth. Ray brought uniformitarianism into the history of plants and animals. Neither Lyell nor Ray told the whole story, but they both helped open the vistas of time, a new world for evolution and its unsolved problems. Ray was among the first to suggest that the fossil shapes found in mountains and within the earth were not mere accidents but the remains of once living creatures. And he followed through with the possibility that many prehistoric species might have become extinct. Which justified his epitaph (translated by someone from the Latin):

> Nor did his artful labours only shew
> Those plants which on the earth's wide surface grew,
> But piercing ev'n her darkest entrails through
> All that was wise, all that was great he knew
> And nature's inmost gloom made clear to common view.

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Specimen Hunting

LINNAEUS inherited Ray's mission. His System of Nature, while more comprehensive and more influential than any before, would be built from elements bequeathed by Ray. Sharing a faith in the coherence of nature, Linnaeus would promote Natural Theology as much as Natural Science. He too made "species" his clues to the wisdom of the Creator.

But in their personalities and ways of working Ray and Linnaeus had little in common. Ray, the lonely and humble acolyte of his boon companion and fellow scholar Willughby, wrote mainly from his own observation. Linnaeus, sociable and conceited, was a brilliant teacher, inspiring and organizing legions of specimen hunters to scan the world and send him their findings—for the greater glory of God and of Linnaeus.

Like Ray, Carolus Linnaeus (1707–1778) was intended for the ministry. Born in southeastern Sweden to an impoverished pastor who awakened his love of plants in the parsonage garden, Linnaeus was raised in Stenbrohult, which he called "one of the most beautiful places in all Sweden, for it lies on the shores of the big lake of Möckeln. . . . The church . . . is lapped by the clear waters of the lake. Away to the south are lovely beech woods, to the north the high mountain ridge of Taxas. . . . To the northeast are pine woods, to the southeast charming meadows and leafy trees." He never forgot these infectious charms. "When one sits there in the summer and listens to the cuckoo and the song of all the other birds, the chirping and humming of the insects; when one looks at the shining, gaily coloured flowers; one is completely stunned by the incredible resourcefulness of the Creator."

Yet at school Carolus showed so little interest in theology that his disgusted father was about to apprentice him to a shoemaker. A perceptive teacher persuaded the father to let Carolus try to make his way as a medical student. At Uppsala he substituted for the professor doing demonstrations in the university's botanical gardens. Then in 1732 he was sent by the Uppsala Society of Science on an expedition to mysterious Lapland, to gather specimens and information on local customs. This first strenuous

encounter with strange flora and exotic institutions dazzled him with a delight he had never felt so poignantly in neat botanical gardens, nor even in the pages of herbals or bestiaries.

On his return he went to the Netherlands, then a center of medical learning, to qualify himself to make a living as a doctor and also to pursue his botanical ambitions. Within the next three years, even before he was thirty, Linnaeus sketched his grand scheme. His succinct *Systema Naturae* (Leyden, 1735) of only seven folio pages, the first work he published in the Netherlands, was a prospectus for his lifework and for all modern systematic biology. Even before, at Uppsala when he was only twenty-two, he had described the essence of his system to the professor with whom he was living. His New Year's Day greetings then apologized for his inability to offer the customary verse. " 'Poets are born, not made,' I was not born a poet, but a botanist instead, so I offer the fruit of the little harvest which God has vouchsafed me. In these few pages is handled the great analogy which is found between plants and animals, in their increase in like measure according to their kind, and what I have here simply written, I pray may be favorably received." His botanical system was possible because, like Ray, he was not looking at plants alone. But going beyond Ray, he boldly adapted a concept from the animal world for the whole living creation.

Linnaeus was the Freud of the botanical world. With our late twentieth-century freedom to discuss sexuality, we forget the embarrassment in "mixed company" in the pre-Freudian age at public mention of any sexual organs, even though they were only those of plants. In Linnaeus' botany, as in Freud's psychology, the primary fact was sexuality.

Ever since Ovid, poets had played with the metaphor of sexuality in plants. But most people still regarded such suggestions in prose to be perverse, if not obscene. A few naturalists had hinted at and some had dared to demonstrate the phenomenon. The French botanist Sebastien Vaillant (1669–1722), in charge of the Jardin du Roi (now called the Jardin des Plantes), using the peculiarities of the pistachio tree that still stands in its Alpine garden in Paris, had boldly opened his public lectures in 1717 with a demonstration of the sexuality of plants, which awakened the adolescent Linnaeus' interest and set him scrutinizing every plant to count its genital organs.

Some decades before, the essential fact had been revealed by a German botanist, Rudolph Jacob Camerarius (1665–1721), who showed that a seed would not germinate without the cooperation of pollen. But when Linnaeus was a student at Uppsala, the sexuality of plants was still an open and very sensitive question. In the title of his paper, *Sponsalia Plantarum* (1729), he used the discreet language of metaphor—"an Essay on the betrothal of plants, in which their physiology is explained . . . and the perfect analogy

with animals is concluded." Just as in the spring the sun animates and enlivens the dormant bodies of animals, so plants, too, he said, wake up from a winter sleep. Plants, like animals, are barren when young, are most fertile in middle years, and waste away in old age. With the microscope, he noted, Malpighi and Nehemiah Grew (1641–1712) had recently shown that plants, like animals, really had differentiated parts. Was it not only logical that they, too, should have organs of generation?

Vaillant had located these organs in the flower, for he said that no fruit was ever produced without a flower. But, the young Linnaeus objected, the botanists who had focused on the corolla or petals were not quite right, because some plants did bear fruit even though they had neither calyx nor petals. The generative organs, Linnaeus ventured, which ought to be the basis of classification were, rather, the stamens and the pistils, whether found on the same or on different plants of the same species. In a cloying passage designed to satisfy the most reverent or the most squeamish, he gives us a clue to the inhibitions of his age. The petals of a flower, he explained, did not directly aid the process of generation. But their attractive shapes and colors, perfumed with appealing odors, had been devised by an ingenious Creator so that the "bridegrooms" and the "brides" of the plant kingdom could celebrate nuptials in their own delightful "bridal beds."

When he arrived in the Netherlands, Linnaeus was already equipped with the data from his field trips and his metaphor of a "sexual system" to make his grand outline. In those seven folio leaves of his *Systema Naturae,* he drew on Ray's notion of species and made each self-generating group of plants a building block. If the self-generating species was basic, it was natural that in Linnaeus' system the generative or "sexual" apparatus of each plant should be the hallmark of classification.

In the details of Linnaeus' argument we begin to see both the boldness of his emphasis on sexuality and why some contemporaries called him salacious. The twenty-three *classes* of flowering plants were distinguished on the basis of the "male" organs (i.e., the relative length and number of the stamens). His twenty-fourth *class (Cryptogamia),* of the plants like mosses which appeared flowerless, were distinguished into *orders* on the basis of their "female" organs (the styles or stigmas). He made up their names from Greek words with plain sexual and generative overtones, drawing on such Greek words as *andros* (male), *gamos* (marriage), *gyne* (female). He described the class *Monandria* as like "One husband in a marriage," the *Diandria* as "Two husbands in the same marriage." The poppy *(Papaver)* and the linden *(Tilia),* being *Polyandria,* he observed, showed "Twenty males or more in the same bed with the female." His *Philosophia Botanica* (1751) continued to insist on the calyx as a nuptial bed

(thalamus) with the corolla acting as a decent curtain *(aulaeum).* "The calyx," he said, "might be regarded as the *labia majora* or the foreskin; one could regard the corolla as the *labia minora.*" "The earth is the belly of the plants; the *vasa chylifera* are the roots, the bones the stem, the lungs the leaves, the heart the heat; this is why the ancients called the plant an inverted animal." He advised "those who want to penetrate further into the mystery of the sex of plants" to consult his *Sponsalia Plantarum.*

We cannot be surprised that proper professors were troubled by such explicitness. But not Erasmus Darwin (1731–1802), the grandfather of Charles, who soon cast the Linnaean system into a grand epic of heroic couplets, *The Botanic Garden* (1789, 1791). There he described "the Ovidian metamorphosis of the flowers, with their floral harems," the impatient male stamens (belonging to floral beaux, lovers, swains, husbands, and knights) pursuing the recumbent pistils (belonging to virgins, wives, and nymphs). In the lily flower of the *Colchicum* genus:

> *Three* blushing maids [pistils] the intrepid nymph attend
> And *six* youths [stamens], enamour'd train! defend

The flower of turmeric *(Curcuma),* a tropical plant of the ginger family, which Linnaeus had distinguished by its one fertile stamen and its four sterile stamens, was where,

> Woo'd with long care, Curcuma cold and shy
> Meets her fond husband with averted eye:
> Four beardless youths the obdurate beauty move
> With soft attentions of Platonic love.

Other readers did not find it so easy to etherealize Linnaeus. Even an accomplished botanist like the Reverend Samuel Goodenough (1743–1827), a vice-president of the Royal Linnaean Societies who had a plant, goodwinia, named after him, could not conceal his embarrassment at "the gross prurience of Linnaeus' mind. . . . A literal translation of the first principles of Linnaean botany is enough to shock female modesty. It is possible that many virtuous students might not be able to make out the similitude of *Clitoria.*" As late as 1820, even the iconoclastic Goethe was still hoping that young people and women could be shielded from Linnaeus' gross "dogma of sexuality."

The motives behind Linnaeus' sexual system were not mere convenience or prurience. Self-generating species were essential to an all-wise Creator's self-generating nature in which all the units would continue to fit together.

Linnaeus shared both Aristotle's belief in some intelligible underlying order and Aristotle's love of facts. The varied devices by which the Creator had provided for the perpetuation of the system were an awesome spectacle.

Besides his debt to Camerarius, Linnaeus owed most to Andrea Cesalpino, who had directed the botanical garden in Pisa before he became physician to Pope Clement VIII in 1592. A thorough Aristotelian, Cesalpino believed that plants were animated by a vegetable "soul" which both nourished and reproduced them. Their nutrition came entirely from roots in the soil, then up through the stem into the fruit. Cesalpino suggested a classification based on general outward structure—roots, stems, and fruit. He thus avoided altogether the problem of classifying the "lower" plants like lichens and mushrooms, which he believed to lack organs, including those for reproduction, found in higher plants, and which, he explained, sprang by spontaneous generation from putrefying matter. Still, Cesalpino's focus on the general structure of individual plants was a long step forward.

The dominant Aristotelian tradition, as we have seen, had begun from large *a priori* categories based on gross preliminary impressions. Ray's historic departure was to make the *species* his elementary unit. In the modern incremental style, Linnaeus, carrying on with Ray, built up his system from the individual species, which could be scrutinized in specimens. With stamens and pistils as starting points, he used the number and order of stamens to group all plants into twenty-four classes, then according to the number of pistils he subdivided each class into orders. This simple plan was easy to use in the field, and even without a library anyone who could count could classify a plant.

While the "sexual" system provided a simple classifying concept, the nomenclature of biology was still cumbersome, vague, and variant. A growing worldwide community of naturalists would need a common language to be sure they were talking about the same thing. Linnaeus would invent the syntax. Efforts to create other sorts of international language had never had such success. But Linnaeus managed to create an international language, a kind of Esperanto of biology. So he found a universal use for Latin long after it had ceased to be the European language of learning. His "botanical Latin" was based not on classical Latin but on medieval and Renaissance Latin, which he reshaped for his purpose.

In retrospect the binomial nomenclature (e.g., *Homo sapiens,* for genus and species) seems so simple and obvious that it hardly needed to be invented. But before Linnaeus devised his binomial scheme, there was no generally agreed-upon scientific name for any particular plant. The earlier names affixed by different writers aimed to serve both as designation and

as description. When more species came to be known and more was known about each plant, names became longer and more confused. Take, for example, the plants of the genus *Convolvulus,* trailing plants of the morning-glory family with funnel-shaped flowers and triangular leaves. In 1576 the French botanist Charles de Lécluse (1526–1609) designated one species as *Convolvulus folio Altheae.* In 1623 the Swiss botanist Gaspard Bauhin (1560–1624) called this same species *Convolvulus argenteus Altheae folio,* which in 1738 Linnaeus amplified to *Convolvulus foliis ovatis divisis basi truncati: laciniis intermediis duplo longioribus,* which by 1753 he had elaborated further into *Convolvulus foliis palmatis cordatis sericeis: lobis repandis, pedunculis bifloris.* And so it went.

Linnaeus came to his solution only gradually, in a search for accurate names that would be usable in the field and handy for the amateur. He did not expect his students on field trips to learn or remember the full Latin description. He did expect them to remember the name of the genus (in the above case, *Convolvulus)* and then in their notes record a number (e.g., "Convolvulus No. 3") referring to the entry for that species in the full list of plants that Linnaeus had published. This gave a hint for a simple binomial system, which could be produced by substituting a word for the number.

The obstacle again was Linnaeus' temptation to make each plant's specific name serve both as a label and as a description. His great simplifying decision was to split these two functions. He would provide only a short, easy-to-remember label. This the student could use when he returned to his library, where it would lead him to a detailed account of the distinguishing features of that species. In the 1740's he tried this for a few plants, but he still stigmatized these as "trivial names" *(nomina trivialia).* To use the species name along with the genus, Linnaeus said, was "like putting the clapper in the bell." Then in his epochal *Species Plantarum* (1753), after twelve months of intensive labor, he supplied such binomial labels for all the fifty-nine hundred species on his list.

Linnaeus wisely realized that it was better to have some handy distinctive name for each species at once than to wait until the perfect word or a thoroughly symmetrical vocabulary could be found. He had to move quickly if he was to accomplish his task at all. Unless he speedily gave some such binomial label to *every* known species, naturalists would be tempted to use the same name for more than one species, which of course would have defeated the whole scheme. His was a monumental task of hasty linguistic invention. He ransacked his Latin for enough terms to make up thousands of labels, sometimes using a single word describing a plant's manner of growth (e.g., *procumbens*), other times using a word for the habitat or for

the first discoverer of the plant, or even a Latinized form of a vernacular word. Linnaeus was not too rigorous in the logic of his usage, provided the word was distinctive and rememberable.

When, a few years later, in the definitive tenth edition of his *Systema Naturae* (1758–59) he extended his scheme to animals, Linnaeus showed a similar practical sense. For insects he used specific names designating color or the host plant. To distinguish species of butterflies, he drew on his copious classical learning, and added such epithets as Helena, Menelaus, Ulysses, Agamemnon, Patroclus, Ajax, or Nestor. Then again, in deference to vernacular usage he set up the genus *Felis,* included the lion, tiger, leopard, jaguar, ocelot, cat, and lynx, and designated them by their common Latin names, Leo, Tigris, Pardus, Onca, Pardalis, Catus, and Lynx.

When was there another such colossal feat of name-giving since the Creation? Any parent who has had to name a child can imagine the enormous task of christening that Linnaeus completed in a single year. Within a few decades, even before his death in 1778, his names and his scheme of naming were adopted by his European colleagues. His choices proved themselves over the centuries and would reach across the world. Linnaeus made a world community of naturalists.

The Age of Discovery, meanwhile, had vastly widened the Europeans' vision of nature. From Asia, Africa, Oceania, and the Americas came news of strange plants like the tomato, maize, the potato, cinchona, and tobacco, and new animals like the penguin or "magellanic goose," the manatee, the dodo, the horseshoe crab, the raccoon, the opossum, and countless others.

Linnaeus inspired an unprecedented worldwide program of specimen hunting. His work gave generations of specimen hunters a new incentive to advance science, even at the risk of their lives. No longer would their hard-won finds be relegated to attics or buried in the meaningless jumble of "cabinets of curiosities." Now every plant or animal newly "identified" by Linnaeus' system contributed to a systematic worldwide survey.

Linnaeus himself commanded cohorts of his apostles—his cleverest pupils, "the true discoverers . . . as comets among the stars," who covered the earth. In 1746 his ablest student, Christopher Tärnström, begged to be allowed to go (with free passage on a Swedish East India Company ship) as Linnaeus' emissary to gather specimens in the East Indies. When Tärnström died of a tropical fever on arriving in the Sea of Siam, Linnaeus futilely tried to make amends to the distraught widow and children by naming a tropical genus *Ternstroemia.*

Peter Kalm, another student, had better luck. Linnaeus secured financing for Kalm's costly travels from a group of Swedish manufacturers and from the universities of Uppsala and Åbo. An expedition to lands in the same

latitude as Sweden would find new plants to be grown in Sweden for medicine, food, or manufacture. The imported red mulberry, they hoped, would feed silkworms for a whole new industry. These hopes never materialized, but Kalm otherwise proved to be one of the most productive of the specimen hunters. In 1748 after a rough Atlantic crossing, the indefatigable Kalm arrived in Philadelphia, visited his fellow Swedes in Delaware, then with help from Benjamin Franklin and two of Linnaeus' best correspondents, John Bartram and Cadwallader Colden, he explored Pennsylvania and went north to New York and Canada. Linnaeus eagerly awaited the botanical finds, and when Kalm arrived back in Stockholm in 1750, the gout-ridden Linnaeus leaped from bed to greet his adored pupil. Three years later Linnaeus' *Species Plantarum* cited Kalm as his source for ninety species, sixty of them new, and he immortalized Kalm in a whole mountain-laurel genus, *Kalmia.* Kalm's journal, which prophesied American independence, gave one of the most vivid descriptions of colonial life in the New World.

Frederick Hasselquist (1722–1752) was sent with money raised by Linnaeus to Egypt, Palestine, Syria, Cyprus, Rhodes, and Smyrna—all still unexplored by European naturalists. When his expenses exceeded his budget, Linnaeus persuaded the Swedish Senate to make private contributions. And when Hasselquist, still only thirty, died near Smyrna, his creditors refused to release his botanical notes until his debts were paid. Again Linnaeus came to the rescue by inducing the Queen of Sweden to pay off the debts. And when he finally read the journals of his deceased disciple, he was ecstatic. "They penetrate me as God's word penetrates a deacon. . . . May God grant that Her Majesty has them published as soon as possible, so that all the world may taste the pleasure I had yesterday." Linnaeus himself published the *Iter Palaestinum* in 1757, and the world could soon enjoy Hasselquist's discoveries through translations in English, French, German, and Dutch.

To China in 1750 he dispatched another pupil, Pehr Osbeck (1723–1805), as ship's chaplain. "On your return," he wrote, "we will make crowns with the flowers you bring back, to adorn the heads of the priests of the temple of Flora and the altars of the goddess. Your name shall be inscribed on substances as durable and indestructible as diamonds, and we will dedicate to you some very rare *Osbeckia* which will be enrolled in Flora's army. So —hoist your sails and row with all your might; but take heed not to return without the choicest spoils, or we shall invoke Neptune to hurl you and all your company into the depths of the Taenarum." Osbeck heeded the warning, and on his return he delivered to his mentor a rich Chinese herbarium of six hundred specimens.

Nearer home, when the King of Spain requested a Linnaean disciple for a botanical survey of his country, Linnaeus sent "his most beloved pupil,"

Petrus Löfling (1729–1756), who had been living with Linnaeus as companion to his son. Löfling's work in Spain stimulated an expedition to Spanish South America, with Löfling as chief botanist, aided by two surgeons and two artists, "to collect specimens for the Spanish Court, the King of France, the Queen of Sweden, and Linnaeus." But, before Löfling could complete his mission, he died of a tropical fever in Guiana at the age of twenty-seven. "Löfling sacrificed himself for Flora and her lovers," Linnaeus lamented, "they miss him!"

The troubled Linnaeus asked, "The deaths of many whom I have induced to travel have made my hair grey, and what have I gained? A few dried plants, with great anxiety, unrest, and care." Still, during the last thirty years of his life he continued to enlist, organize, and dispatch his apostles around the world. In 1771, he surveyed his messianic strategy:

> My pupil Sparrman has just sailed for the Cape of Good Hope, and another of my pupils, Thunberg, is to accompany a Dutch embassy to Japan; both of them are competent naturalists. The younger Gmelin is still in Persia, and my friend Falck is in Tartary. Mutis is making splendid botanical discoveries in Mexico. Koenig has found a lot of new things in Tranquebar [in south India]. Professor Friis Rottböll of Copenhagen is publishing the plants found in Surinam by Rolander. The Arabian discoveries of Forsskål will soon be sent to the press in Copenhagen.

Linnaeus' worldwide movement gained momentum with the years. Answering a request from England, he sent another favorite pupil, Daniel Solander (1736–1782), who became his link to the expeditions of the next centuries. Solander charmed his way up English society, then became librarian to Sir Joseph Banks (1743–1820), who was the European patron of natural history in the next generation. Banks promoted, organized, and personally financed natural-history expeditions, and, as we have seen, took Solander along on Captain Cook's *Endeavour* voyage (1768–71) around the world. But Linnaeus was disappointed in Solander, who, despite Linnaeus' schemes, never married his eldest daughter, and then from the round-the-world voyages "the ungrateful Solander" never sent Linnaeus a single plant or insect. Banks, who had covered Solander's expenses and had bought costly equipment, was also disappointed. For he had hoped that Linnaeus would be willing to come to England to help give names to the finds of the voyage—twelve hundred new species and one hundred new genera of plants, with many more animals, fishes, insects, and mollusks.

After Solander's work with Banks it became customary for every exploring ship to carry a naturalist, along with an artist to depict the finds. As a botanist on his second voyage around the world, Captain Cook chose

another Linnaeus pupil, the young Anders Sparrman (1748–1820), who at the age of seventeen had already gone to China as surgeon on a Swedish East India ship and brought back a treasury of specimens. After returning from Cook's voyage, Sparrman carried his botanical searches into Senegal and the west coast of Africa.

One of the most enterprising apostles was Carl Peter Thunberg (1743–1828), the last of his disciples promoted by Linnaeus himself. At the time the Dutch, on their tiny trading post on the island of Deshima in Nagasaki Bay, were the only Europeans with a foothold in Japan. To catalogue the flora of Japan, Thunberg would have to secure the protective coloration of a Dutchman. Therefore he spent three years in Cape Colony learning Dutch. Incidentally, while he was there he voyaged into the interior, and described three thousand plants, of which about one thousand were new species. In 1775, when he arrived on a Dutch ship at Deshima, the only excursion he was permitted was to accompany the Dutch ambassador on his annual ceremonial visit to the Emperor in Tokyo. Luckily, the young Japanese interpreters on Deshima turned out to be physicians eager to learn European medicine, morsels of which Thunberg exchanged for specimens of Japanese plants. When Japanese servants brought fodder from the mainland for the cattle on Deshima, Thunberg would rummage through it to find specimens for his herbarium. After nine years' absence, Thunberg finally returned to Sweden where he grieved to find that his mentor had died the year before.

In the next generation the unauthorized apostles of Linnaeus were an energetic crew. Pursuant to the custom established by Solander, Sparrman, and Thunberg, the twenty-two-year-old Darwin was enlisted in 1831 as naturalist on H.M.S. *Beagle.* In 1846 the persuasive Thomas Henry Huxley, who had gathered specimens as assistant surgeon on H.M.S. *Rattlesnake* in the South Seas, set a precedent when he secured three years' leave on Navy pay to analyze his finds. The brilliant young Joseph Dalton Hooker (1817–1911), who was carried as assistant surgeon and naturalist on Captain James Clark Ross' expeditions to the Antarctic (1839–43) on H.M.S. *Erebus* (with H.M.S. *Terror*), produced six volumes on polar flora which secured him a Navy commission to study the flora of the Himalayas and Ceylon, and finally made Kew Gardens a world center for botanical research.

The same faith that nourished Linnaeus' quest for a "system" in nature also had convinced him that it was impossible for any man fully to grasp the plan of his Creator. He knew very well that his "sexual" scheme was artificial, only a handy way to file specimens. A strictly *natural* classification would have to group together plants that shared the largest number of attributes.

Linnaeus showed common sense when he seized on Ray's concept of

"species" as a useful handle on the whole creation. But he was not above using his theology to validate his vocabulary of convenience. "We can count as many species now," was Linnaeus' most quoted aphorism, "as were created in the beginning." The constancy and permanency of species was, of course, essential to justify the trouble of classification. Why bother to file plants in different species if at any time they could slide into another species or disappear without warning?

As Linnaeus' disciples gathered more thousands of "species," with more examples of hybridization, he began to venture the possibility that in the beginning perhaps not quite *all* species had been created. Perhaps new species could arise later by the combination of the primordial species of one genus with a species of another genus. This opened some chaotic possibilities, and when Linnaeus occasionally speculated on the origins of species, he went off the deep end. Luckily, religious faith and a practical temperament kept him from plaguing himself with origins—probably knowable anyway only by the Creator. "*Deus creavit, Linnaeus disposuit*"—God created, Linnaeus classified—his admirers boasted, with only a hint of blasphemy.

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Stretching the Past

AMONG the learned in the Europe of their day, it would have been hard to find a sharper contrast to Linnaeus than his aristocratic contemporary Georges-Louis Leclerc, Comte de Buffon (1707–1788). In retrospect they seem allies in the discovery of nature, but in their own time they were notorious antagonists. Perhaps his youth in a poor rural parsonage had led Linnaeus to insist that nature must consist of changeless building blocks "as many as were created in the beginning." Buffon spoke for an urbane world of change. Born into a monied family in Burgundy, where his father was an officer of the bureaucratic nobility, Buffon was educated at a good Jesuit college and the University of Dijon, where he pursued his father's ambition that he become a lawyer. Then, at the University of Angers, he turned to medicine, botany, and mathematics. After a duel he had to leave the university, and he took off on a Grand Tour in the suitable company of the Duke of Kingston and the Duke's tutor, who happened to be a member of the

Royal Society. Returning home, Buffon found that his mother had died, and that his father had remarried and had seized the rich estates which should have come to him from his mother's side. After a bitter quarrel with his father with whom he was never again on speaking terms, he managed to secure for himself the ample estates, including the village of Buffon, which gave him his noble name. The twenty-five-year-old Buffon promptly set himself up as a provincial lord.

Meanwhile he vigorously pursued his scientific interests. In Paris, Buffon first became known for his report to the Navy on the tensile strength of timbers used in ships of war. A paper on probability theory, which brought him *adjoint-mécanicien* membership in the French Academy, was followed by works on mathematics, botany and forestry, chemistry and biology. He used the microscope for his research on the organs of animal reproduction. He translated into French Stephen Hales' *Vegetable Staticks* and Newton's work on the calculus. At twenty-eight, for his impressive attainments he was recognized by the King, who named him superintendent of the royal botanical gardens.

For fifty years Buffon spent spring and summer on his estates in Burgundy, fall and winter in Paris. In the country, rising at dawn, he gave mornings to science, afternoons to business. In his evenings in Paris he charmed the wittiest hostesses in salons, where, as William Beckford acidly recorded, "Zoology, Geology, and Meteorology formed the chief topics discussed, but tautology prevailed over all." After a half-century of this routine he not only was rich from his increased landholdings but had doubled the area and enlarged the buildings of the royal botanical gardens, and had published thirty-six volumes of his *Histoire Naturelle* and scores of important articles on every branch of science. Louis XV made him the Comte de Buffon, Catherine the Great honored him, and he was elected to scientific academies in London, Berlin, and St. Petersburg.

Buffon's fame reached America, which had joined the expanding European community of science. Thomas Jefferson, stationed in Paris in 1785 as American minister to France, had the Marquis de Chastellux deliver to Buffon a copy of his *Notes on Virginia,* just off the press, along with a large American panther skin to contradict Buffon's thesis of the degeneration of animals in the New World. This brought Jefferson an invitation to come discuss natural history and dine in Buffon's gardens. As Jefferson recalled, "It was Buffon's practice to remain in his study till dinner time, and receive no visitors under any pretense; but his house was open and his grounds, and a servant showed them very civilly, and invited all strangers and friends to remain to dine. We saw Buffon in the garden, bút carefully avoided him; but we dined with him, and he proved himself then, as he always did, a man of extraordinary powers in conversation."

At the age of forty-five Buffon married a beautiful girl twenty-five years his junior, who died young. Their daughter died in infancy, and their pampered only son (whom Catherine the Great used as an example of geniuses' sons who are imbeciles) was guillotined by Buffon's enemies during the Terror in 1794. After his wife's death Buffon's only liaison was a platonic affair with his "sublime friend" Madame Necker, wife of the French Minister of Finance. When he was bedridden in the last year of his life, she visited him daily. "M. de Buffon has never spoken to me of the marvels of the earth," she wrote, "without inspiring in me the thought that he himself was one of them."

In an age when the sciences had newly gone public, Buffon was a pioneer of popular science, which required a new view of language. Of course, he read Latin, but he wrote in French, which for him was an act of faith—not glossing texts for a learned few but presenting facts to the nation. "Style is the man himself," he declared in his classic *Discours sur le Style* (1753), delivered on his reception into the French Academy. He was suspicious of writers who refined their subtleties, whose thought was "like a leaf of hammered metal, acquiring luster at the expense of substance." Rousseau called him the most beautiful stylist, and his lyrical prose (he wrote no verse) led some to place him among the leading French "poets" of his century.

The thirty-six volumes of Buffon's *Histoire Naturelle* (1749–85), which appeared during his lifetime, supplemented by eight volumes published (1788–1804) after his death, covered every subject in nature from man and birds to cetaceans, fishes, and minerals. For the first time in publishing history, books of popular science were best sellers. His work rivaled Diderot's thirty-five-volume *Encyclopédie* (1751–72), the most successful European publishing venture of the century, which gave its name to the age. Diderot's work was conspicuously collaborative, Buffon's, despite some assistance, was unquestionably his own.

Buffon took aim at the large audience of laymen. In his famous article on the camel a single Proustian paragraph-sentence recaptured the desert (as we can see in this translation by Otis E. Fellows and Stephen F. Milliken):

> Try to imagine a country without greenery and without water, a burning sun, a sky always dry, sandy plains, mountains more arid still, over which the eye sweeps in vain and sight is lost without once fixing upon a living object; a dead land, as though stripped bare by the hot wind, offering to the eye only the remnants of bones, scattered stones, outcroppings of rock, upright or fallen, a desert without secrets in which no traveler has ever drawn a breath in the shade, or found a companion, or anything to remind him of living nature: absolute solitude, a thousand times more terrifying than that of the dense forests, for trees

> are other beings, other life, to the man who sees himself alone; more isolated, more naked, more lost, in these empty and limitless lands, he stares into space, on all sides, space that is like a tomb; the light of day, more melancholy than the shadows of night, is reborn only to shine upon his nakedness and impotence, to let him see more clearly the horror of his situation, driving back the boundaries of the void, extending around him the abyss of the immensity that separates him from the land of men, an immensity that he will attempt in vain to cross, for hunger, thirst, and the scorching heat press upon every moment that remains between despair and death.

Yet his descriptions of some animals were so concise that they were collected to make books for children.

While the stark sexual nomenclature of Linnaeus had simply shocked, Buffon found romance in the sexual activity of his animals. For example, he contrasted the mating of sparrows and of pigeons.

> There are few birds as ardent, as powerful in love as the sparrow; they have been seen to couple as many as twenty times in succession, always with the same eagerness, the same trepidation, the same expression of pleasure; and, strange to say, the female seems to grow impatient first with a game that ought to tire her less than the male, but it can please her also much less, for there are no preliminaries, no caresses, no variety to the thing; much petulance without tenderness, movements always hasty, indicative only of a need to be satisfied for its own sake. Compare the loves of the pigeon to those of the sparrow, and you shall see almost all the nuances that extend from the physical to the moral.

Meanwhile, among the pigeons,

> tender caresses, soft movements, timid kisses, that become intimate and urgent only at the moment of enjoyment; this moment even, brought back within seconds by new desires, new approaches equally nuanced; an ardor ever durable, a taste ever constant, and a still greater benefit, the power to satisfy them repeatedly, without end; no bad temper, no disgust, no quarrel; an entire lifetime devoted to the service of love and to the care of its fruits.

His work was emphatically not a "system" but a description, "a natural history."

Since the unity that Buffon saw was in the processes of nature, he was wary of nomenclature, whether provided by God or by Linnaeus. It is not surprising that Linnaeus became his *bête noire.* Buffon believed that taxonomy was just a learned technique for making the world seem simpler than it really was. By using stamens to classify plants, Linnaeus had put the veneer of a word over what was really a miscellany. Surely, eyes were given man to distinguish plants from one another, yet Linnaeus' artificial scheme

depended on features so minute they could be seen only with a microscope. Buffon concluded that Linnaeus' "system" had actually "made the language of science more difficult than science itself!"

Taxonomy and nomenclature, Buffon warned, were only games. His own "true method" was simply "the complete description and exact history of each thing in particular." "One must not forget that these *families* [confidently used by Linnaeus and others] are our creation, we have devised them only to comfort our own minds." To grasp all distinctive features of a particular individual, it is not enough to describe only the individual in hand. We must try to envisage everything about that animal, which means compiling the history "of the entire species of that particular animal . . . their procreation, gestation period, the time of birth, number of offspring, the care given by the mother and father, their education, their instincts, their habitats, their diet, the manner in which they procure food, their habits, their wiles, their hunting methods."

Without any pretense at knowing how many "species" God had created "in the Beginning," Buffon, following Ray's lead, satisfied himself with a purely empirical definition:

> We should regard two animals as belonging to the same species if, by means of copulation, they can perpetuate themselves and preserve the likeness of the species; and we should regard them as belonging to different species if they are incapable of producing progeny by the same means. Thus the fox will be known to be a different species from the dog, if it proves to be the fact that from the mating of a male and a female of these two kinds of animals no offspring is born; and even if there should result a hybrid offspring, a sort of mule, this would suffice to prove that fox and dog are not of the same species—inasmuch as this mule would be sterile.

Mere external resemblance would not prove animals to be of the same species "because the mule resembles the horse more than the water spaniel resembles the greyhound."

Yet he was awed by the very concept of species, and wary of oversimplifying its nuances. His diffidence was much deeper than that of his predecessors. Buffon could not bring himself to believe that "species" provided a key to any divine scheme or a clue to theological truth.

> In general, the kinship of species is one of those profound mysteries of nature which man will be able to fathom only by means of long and repeated and difficult experiments. How, save by a thousand attempts at the cross-breeding of animals of different species, can we ever determine their degree of kinship? Is the ass nearer to the horse than to the zebra? Is the dog nearer to the wolf than to the fox or the jackal? At what distance from man shall we place the great apes, which

> resemble him so perfectly in bodily conformation? Were all the species of animals formerly what they are today? Has their number not increased, or rather, diminished? . . . How many more facts we shall need to know before we can pronounce —or even conjecture—upon these points! How many experiments must be undertaken in order to discover these facts, to spy them out, or even to anticipate them by well-grounded conjectures!

The Bible had, of course, disposed of all such troublesome problems in the six days when God created heaven and earth "and every living creature which moveth." Respectable biologists, including Ray and Linnaeus, had made this their point of departure. Since it was an axiom that species could not be either added or subtracted, the precise extent of time since the Creation held little significance for the biologist. Biblical scholarship in the seventeenth century kept biologists focused on those six days of Creation. It seemed both absurd and heretical to suggest that nature had a history. What interested Biblical scholars was the chronology of the Bible in relation to human events.

The Irish prelate James Ussher (1581–1656), an expert in Semitic languages, managed to provide for the first time a generally acceptable Biblical chronology, still found in many editions of the English Bible. A scholar of Trinity College, Dublin, he became a fellow, went to England to collect books for the college library, and then became professor of divinity and archbishop of Armagh. While strident in demanding autonomy for the Church of Ireland, he won the respect of fellow Protestants in England by his scholarly polemics against Rome. In his search for authentic Biblical texts he hired his own agent to gather manuscripts in the Middle East and collected a famous library, which included the Book of Kells. Some of his distinctions between spurious and authentic texts are still accepted by Biblical scholars today. In 1654 he delivered the fruits of his lifetime of scholarship when he declared that the Creation had occurred on October 26, 4004 B.C., at 9:00 A.M.

The precision of this discovery and Archbishop Ussher's prestigious documentation added weight to the widespread belief that the earth and all living creatures had been created within a single week only a few thousand years before the Christian era. This view of the Creation confined biological history to what, by modern geological standards, is a relatively brief time. This brevity itself seemed to confirm the dogma that no species could have been added, nor any have become extinct, and so was a congenial setting for the belief in the fixity of species which made possible Linnaeus' System of Nature.

For geology the brevity of earthly time had an additional consequence, which was in every sense of the word catastrophic. It encouraged a belief

in sudden changes, a doctrine known as "catastrophism." Of course everybody could see that weather and climate were still slowly changing the forms of the earth by deepening streams, flooding valleys, and eroding mountains. Herodotus, Strabo, and Leonardo da Vinci had described these processes. But it was generally agreed that in the mere six thousand years since the Creation the flow of water and the crumbling of rocks could not possibly have produced the drastic changes now visible in all the varied landforms. Orthodox naturalists were therefore driven to explain large changes in earth forms by sudden cataclysms, or "catastrophes."

Buffon, not satisfied either by Archbishop Ussher's calculations or by the glib explanations of the catastrophists, plunged into his own study of the earth's dynamism with a naïve experimental enthusiasm. To understand the history of plants and animals, he said, we must first grasp the history of the earth. So Buffon set out to explain how the earth had come into being. Newton, his inspiration in many other ways, had asserted that the six planets, revolving in the same plane in concentric orbits in the same direction, must have been created by God himself. Buffon demanded natural causes, and he came up with his own explanation. "In order to judge what has happened, or even what will happen," he observed, "one need only examine what is happening. . . . Events which occur every day, movements which succeed each other and repeat themselves without interruption, constant and constantly reiterated operations, those are our causes and our reasons."

Buffon's clue for the origin of the earth was Newton's observation that "comets occasionally fall upon the sun." When one such comet collided with the sun, Buffon speculated, fragments of the sun must have been knocked off into space. These liquids and gases (1/650 of the sun's mass) then came together to form spheres revolving in the same direction and in the same plane. Each of them became a planet turning on its own axis, flattened at the poles. And satellites were thrown out.

How did Buffon's new view of the making of the earth affect the extent of historical time? Newton, of course, would not tolerate such an un-Godly account of the Creation. But in the *Principia* Newton had offered some interesting speculations on the rate of cooling of comets. "A globe of red-hot iron equal to our earth, that is, about 4,000,000 feet in diameter," he observed, "would scarcely cool in an equal number of days, or in above 50,000 years." Due to "some latent causes," Newton had ventured, the rate of cooling might be even slower, less even than the ratio of the diameter, "and I should be glad that the true ratio was investigated by experiments." For Buffon, this question held the secret of the age of the earth. If only he could find out precisely how long had been required for the planetary globes to cool down to a habitat suitable for life! He would try.

In his own foundry Buffon cast two dozen globes, one inch in diameter, to be removed white-hot from the furnace. He would then measure the time precisely to "the moment when one could touch them and hold them in one's hand." The answer to his question would come simply by extrapolating that figure to a globe the size of the earth. Even so prosaic an experiment could fire the salacious imagination of these French contemporaries of the Marquis de Sade. As one of Buffon's secretaries recorded, "To determine the epoch of the formation of the planets and to calculate the cooling time of the terrestrial globe, he had resort to four or five pretty women, with very soft skins; he had several balls, of all sorts of matters and all sorts of densities, heated red hot, and they held these in turns in their delicate hands, while describing to him the degrees of heat and cooling." A less sensational report portrayed Buffon himself with one hand holding a watch, the other in a glove cautiously testing the heat of each sphere until he could remove his glove and touch the sphere without being burned.

What Buffon learned in this way about the rates of cooling of spheres he applied to a sphere the size and composition of the earth. And he came up with some bold, theologically dangerous conclusions. "Instead of the 50,000 years which he [Newton] assigns for the time required to cool the earth to its present temperature, it would require 42,964 years and 221 days to cool it just to the point at which it ceased to burn." By further calculations he added to this figure all the years since the earth had cooled to its present temperature, which brought the total age of the earth to 74,832 years.

To his mathematically minded age Buffon was thus able to offer an experimentally verified figure whose precision rivaled the pious calculations of Archbishop Ussher. Modern geologists have, of course, extended this figure into the billions of years. Buffon himself dared observe that "the more we extend time, the closer we shall be to the truth." He had thought of three million years or more, even up to infinity. But he prudently scaled this down, he himself explained, because he did not want to shock readers so much that they might suspect him of pure fantasy. His figure needed to be only enough longer than Archbishop Ussher's to make plausible his modern vista—a world of slow and constant change.

To Buffon the earth no longer seemed the product of one relatively recent Act of Creation. Linnaeus in the ancient taxonomic tradition had focused on the classifiable products of Creation. Buffon would focus on process. The earth would have its own history. Then why not also all of nature, including all the "creatures"?

When Buffon went on from his Theory of the Earth in the very first volume of his *Natural History* (1749) to his *Epochs of Nature* (1779), the fruit of his thirty-year encyclopedic study, he found by a happy coincidence that his vastly extended calendar was divided into precisely *seven* epochs. Which

gave a hitherto unsuspected metaphorical meaning to the Book of Genesis. Seven "days" now became seven "epochs."

Buffon's new chronology helped account for many other puzzling facts. In the first epoch the earth and the planets took shape. In the second epoch, as the earth solidified, the great mountain ranges were formed, with their deposits of minerals and "primitive vitreous material." As the earth cooled in the third epoch, gases and water vapors condensed, covering the whole earth with a flood. Fishes and other marine creatures flourished in the deep waters. Chemical processes pulverized the "primitive vitreous material" from the submerged mountains and made sedimentary deposits, which included organic debris like coal. As these waters rushed into the vast subterranean openings left when the earth had cooled, the flood level dropped. In the fourth epoch, when volcanoes erupted, earthquakes shook the earth, and tumbling waters reshaped the lands. In the fifth epoch, still before the separation of the continents, land animals appeared. In the sixth epoch, when the continents separated, the lands received their present shape. Finally, in the seventh, the present epoch, man appeared, heralding a new stage "when the power of man has seconded that of Nature," opening a future of incalculable possibilities.

The residual heat in the globe, a legacy from the sun, explained many things not covered in the Biblical account. For a long period, while the whole earth remained at a tropical temperature, large elephantlike creatures were found in the northern climates of Europe and North America, which incidentally accounted for the huge fossil bones found there. But as the earth cooled, these animals moved south toward the equator. It was this internal heat of the earth that had originally transformed inorganic into organic molecules and so produced the first living creatures. Since these vital powers were proportionate to the heat, the warmer regions of the earth and the warmer periods of history had always produced larger animals.

As animals migrated they adapted to their environments and so produced new varieties. Of the large animals, fewer varieties emerged because they reproduced slowly. But the prolific small mammals, such as rodents and birds, produced countless varieties. The migrations of animals before the separation of the continents explained their distribution across the earth and the fact that only South America has its own fauna.

By opening the gates of time, Buffon opened a new world of change and progress, later to be revealed as a world of evolution. And, incidentally, he opened the way to thoughts of "continental drift." Buffon's heresies, even more obviously than Galileo's, struck at the Creation and the Creator. He invented a whole new category of heresy. If the shape of the earth was so changeful, if old species could become extinct, if new variations could

emerge, the world was precariously fluid. Did this not perhaps imply changing ways to salvation, changing sacraments, and even a changing Church?

In 1749, when the first volume of Buffon's *Natural History* appeared, a committee of the theology faculty of the University of Paris demanded that, to avoid their censure, he clarify certain passages in writing. This he did. "I have extricated myself with great satisfaction," Buffon boasted to a friend. They voted 115 to 5 not to censure his work. "I abandon whatever in my book concerns the formation of the earth, and in general all that might be contrary to the narration of Moses," Buffon had written to the committee, "having presented my hypothesis on the formation of the planets only as a pure philosophical speculation." At the same time Montesquieu's *Spirit of Laws* was similarly investigated, but when Montesquieu refused to reply, his work was condemned. Thirty years later, though Buffon included this pious disavowal in his *Epochs of Nature,* a committee of censorship was again appointed, but under pressure from the King they never produced a report.

Whether from piety or from prudence, Buffon steadfastly refused to be embroiled in theological controversy. "I do not understand theology," he explained in 1773, "and I have always abstained from discussing it." Scrupulous in his observance of Catholic ritual, he set up a chapel at the very foundry where he cast the globes with which he revised the Biblical "days" of Creation. He regularly attended confession, and sought the last rites of the Church at his death. But, unlike the pious Newton, Buffon did not allow his religion to stultify his view of the past. And unlike his militant contemporary Baron d'Holbach (1723–1789), he never declared himself the "personal enemy" of God, nor did he believe that one had to be an atheist to "destroy the chimeras which afflict the human race." If Buffon himself would not choose between his parallel faiths in God and in science, the historian today must not choose for him.

By his bold extension of time, Buffon changed the vocabulary of nature from a status world of rigid forms and fixed entities to a changeful world of matter in motion, of fluid, mobile individuals. Nature, no longer the finished product of a beneficent Creator, was now a name for myriad processes. Theology would be displaced by history.

Without Buffon's extension of time there was no room for a history of nature, as the career of Buffon's brilliant, frustrated predecessor had revealed. Nicolaus Steno (1638–1686), like Leonardo da Vinci, was cursed by his own versatility. Born in Copenhagen, the son of a wealthy Protestant goldsmith, he studied medicine. Frustrated in his ambition for a post at the university, he went off to Paris, where he published a treatise on the anatomy of the brain. In Florence the Duke of Tuscany became the patron of

his scientific work. A spiritual crisis on All Souls' Day, 1667, led him to convert to Catholicism.

When the Accademia del Cimento assigned him to explore the grottoes at Lake Garda and Lake Como, Steno began his pioneer regional geology, the first of its kind in Europe. He had already explained that "figured stones," which Tuscans called *glossopetri,* or stone tongues, really were not sports of nature but the teeth of sharks that had lived under water there in ancient times. Still only thirty, Steno published in 1669 a revolutionary little book, *Prologue to a Dissertation on how a solid body is enclosed by the processes of nature within another solid body,* which came to be called from its Latin title the *Prodromus.* This book was destined to become a primer of modern geology. Generalizing from his geology of Tuscany, he explained why and how crystals, stones, and fossils were found in strata within the earth.

Steno's radical new insight was that the strata of the earth recorded the history of the earth. With a few simple principles, he transformed the earth's surface jumble into a legible archive. His notion was that the strata found in the earth were originally formed of matter precipitated from water, which then fell to form a sediment at the bottom. In his clear diagram, the first known effort to show a geologic section, he described six successive kinds of stratification. What is below, he said, must normally be older than what is found above. Exceptions occur only when lower layers have been disrupted and then filled in by layers from above. Layers formed by volcanic or chemical means were quite different from those formed by mechanical means. So Steno provided rudimentary definitions of sedimentary, igneous, and metamorphic rocks.

But when he touched the history of the earth, Steno was on dangerous ground. The Bible seemed to say that mountains either had been created in the Beginning by God or had simply grown. Steno began by blandly describing fossils as a class of "solids naturally contained within solids," which included all stony substances of organic origin. Fossilization occurred "where the substances of the shell being wasted, a stony substance is come into the place thereof," which meant that there could be fossils not only of bones and shells but even of plants and soft-bodied organisms. To compress all these processes within six thousand years since the Creation, Steno had to make the six days of the Book of Genesis and Noah's Flood account for more than they could bear. Since there was no history of nature, there could be no prehistory. Therefore the large fossil bones found in the Aretine fields outside Florence could not possibly belong to prehistoric animals, but must be the remains of Hannibal's war elephants.

Steno's *Prodromus* was merely the introduction to a larger work that never came, a foundation on which others could build. In London, Henry

Oldenburg, with his sharp eye for seminal works, promptly translated Steno into English in 1671. Meanwhile the versatile Steno's pioneer work in anatomy had brought him fame. The King of Denmark recalled him to be royal physician and professor of anatomy in Copenhagen. When his Catholic faith made trouble for him, he returned to Florence, and with all the enthusiasm of a convert, he abandoned science. Consecrated a priest in 1675, he diverted his energies to a frenetic ecclesiastical career. Within a year Pope Innocent XI made him a bishop, the vicar apostolic and organizer of Catholic propaganda for all northern Europe. A fanatical propagandist, he even wrote to Spinoza hoping to convert him, but Spinoza never answered. Steno's rabid asceticism hastened his death at forty-eight. He was buried with great ceremony in the Basilica of San Lorenzo in Florence, where we can still see his impressive monument.

It was left to Buffon to open the vistas of modern biology by bringing the whole earth and all its plants and animals onto the stage of history. After Buffon it was harder to believe that anything on earth was changeless. He had glimpsed the "mystery" of species. Now there was time and time to spare for varieties of animals to emerge or become extinct, making the whole world a museum of surprising fossils. By stretching the calendar, Buffon widened the stage for the naturalists' imagination. The creation could be observed not merely as a Linnaean panorama in space, but as a continuous drama in time. "Nature's great workman is Time. He marches ever with an even pace, and does nothing by leaps and bounds, but by degrees, gradations and successions he does all things; and the changes which he works—at first imperceptible—become little by little perceptible, and show themselves eventually in results about which there can be no mistake."

58

In Search of the Missing Link

ONE grand master metaphor dominated, perverted, and obstructed European efforts to discover man's place in nature. This was the simple notion of a Great Chain of Being. The whole universe, European scientists and philosophers explained, consists of an ordered series of beings, from the

lowest, simplest, and tiniest at the bottom to the highest and most complex at the top. To the question, "What is man, that thou art mindful of him?" the Psalmist answered (and natural philosophers agreed), "thou hast made him a little lower than the angels, and hast crowned him with glory and honour."

The Chain-of-Being metaphor was pregnant with ambiguities and contradictions. How many links were there in the chain? How different was one link from its neighbor up or down the scale? Answers to such questions presupposed a total knowledge of nature, which was, of course, the exclusive prerogative of the Creator. A figure of speech seemed to tell Alexander Pope in 1734 all that man needed to know of his place in nature.

> Vast chain of being! which from God began,
> Natures aethereal, human, angel, man,
> Beast, bird, fish, insect, what no eye can see,
> No glass can reach; from Infinite to thee,
> From thee to nothing.—On superior pow'rs
> Were we to press, inferior might on ours;
> Or in the full creation leave a void,
> Where, one step broken, the great scale's destroy'd;
> From Nature's chain whatever link you strike,
> Tenth, or ten thousandth, breaks the chain alike.

Since man was infinitely distant from the perfection of his Creator, was there not room above man too for an infinite number of superior beings? Was man only a "middle link" between the lowliest and the highest? If there was indeed a continuous chain, might not man himself differ only infinitesimally from the nearest nonhuman link? And if man partook equally of the material qualities of the beings below him and of the ethereal qualities of those above, was not man condemned to perpetual inner discord? In his unforgettable couplets, Pope observed:

> Plac'd on this isthmus of a middle state,
> A being darkly wise and rudely great,
> With too much knowledge for the sceptic side,
> With too much weakness for the stoic's pride,
> He hangs between; in doubt to act or rest;
> In doubt to deem himself a god or beast;
> In doubt his Mind or Body to prefer;
> Born but to die, and reas'ning but to err; . . .
> Chaos of Thought and Passion all confus'd,
> Still by himself abus'd, or disabus'd;
> Created half to rise, and half to fall,

Great lord of all things, yet a prey to all;
Sole judge of Truth, in endless error hurl'd;
The glory, jest and riddle of the world.

However appealing to poet and metaphysician, the Chain of Being was not much help to the scientist. Though naturalists spoke glibly of the "missing links," they were discouraged from efforts to learn about man from his similarities to the other animals. While the Chain of Being placed man in a continuous chain, it also made him somehow a link uniquely insulated from the forces of nature.

The Chain of Being proved wonderfully flexible and eventually would accommodate an idea of evolution. But at least until the eighteenth century, it described the product and not the process of creation, and was only another way of praising the wisdom and plenitude of the Creator. It described nature in space, and not in time. To discover his place in nature, man would need a sense of history, of how and when all the different species had appeared, and he would need to see how his body was similar to the bodies of the other animals.

Edward Tyson (1651–1708), a prosperous English physician, was well situated and well qualified to open the paths of discovery from natural history to comparative anatomy. He never secured a place alongside Vesalius, Galileo, Newton, or Darwin in the popular pantheon, he shunned controversy and never sought power in the new parliament of science. But what Sir William Harvey was to physiology, Tyson would be to comparative anatomy. Born in Bristol to a wealthy family with a long record of public service, Edward Tyson followed a conventional path—a Bachelor of Medicine degree at Oxford in 1677, then practice in London with his brother-in-law. When he began his anatomical experiments, he became acquainted with Robert Hooke, who illustrated some of his papers and secured his election as a Fellow of the Royal Society in 1679.

As Curator, he was charged with planning demonstrations for the society's regular meetings. He preached the society's modern gospel of incremental science. And he rejoiced at the wealth of facts flooding in from the New World. "New Tracts, new Lands, new Seas are daily found out, and fresh descriptions of unknown Countreys still from both brought in; so that we are forced to alter our Maps, and make anew the Geography of both again. Nor have the discoveries of the Indies more enriched the world of old, than those of Anatomy now have improved both the Natural and Medical Science." But naturalists must not be tempted to slovenly generalizations—"far better a little with accurateness, than a heap of rubbish care-

lessly thrown together. Malpighi in his Silk-worm hath done more, than Jonston in his whole book of Insects." The patient progress of knowledge of the "lesser" world within must equal that of the "greater" world without, by "taking to pieces this Automaton, and viewing asunder the several Parts, Wheels and Springs that give it life and motion."

"The Anatomy of one Animal," Tyson urged, "will be a Key to open several others; and until such time as we can have the whole completed, 'tis very desirable to have as many as we can of the most different and anomalous." He delighted in Swammerdam's ample account of the Ephemeron or May fly, for life could be understood only by "a *comparative* survey."

> Nature when more shy in one, hath more freely confest and shewn herself in another; and a Fly sometimes hath given greater light towards the true knowledge of the structure and the uses of the Parts in Humane Bodies, than an often repeated dissection of the same might have done. . . . We must not therefore think the meanest of the Creation vile or useless, since that in them in lively Characters (if we can but read) we may find the knowledge of a Deity and our selves. . . . In every Animal there is a world of wonders; each is a Microcosme or a world in it self.

One day when Tyson visited the Tower docks and the Lord Mayor's kitchens in his regular search for unusual fish to dissect, a fishmonger offered him a porpoise. This was the only one of the cetaceans (fishlike mammals lacking hind limbs, including whales and dolphins) found in British waters. It was happy for the future of science that this specimen had lost its way up the Thames.

The Royal Society had expressed a special interest in the anatomy of all rarities, and the porpoise had never been anatomized. Tyson's friend Robert Hooke laid out the society's seven shillings sixpence for the 95-pound "fish," which they took to Gresham College for dissection. There Tyson went speedily about his work, enlisting Hooke to help him make drawings as he went along. Tyson's *Anatomy of a Porpess* (1680) revealed the dangers of classifying animals by their exteriors. John Ray had still classified the porpoise as a fish. "If we view a Porpess on the outside," Tyson observed, "there is nothing more than a Fish." But "if we look within, there is nothing less." Its internal anatomy persuaded Tyson that the porpoise was in fact a mammal, similar to land quadrupeds, "but that it lives in the Sea, and hath but two forefins."

> The structure of the *viscera* and inward parts have so great an Analogy and resemblance to those of Quadrupeds, that we find them here almost the same. The greatest difference from them seems to be in the external shape, and wanting feet. But here too we observed that when the skin and flesh was taken off,

> the fore-fins did very well represent an Arm, there being the *Scapula*, an *os Humeri*, the *Ulna*, and *Radius*, and bone of the *Carpus*, the *Metacarp*, and 5 *digiti* curiously joynted. . . .

Tyson's eye for exotic specimens awakened the interest of his colleagues in the Royal Society. They bought an ostrich for him to dissect. He finally offered the society his illustrated dissections (among others) of an American rattlesnake, a Mexican musk-hog, and an opossum, which had been presented to the society by William Byrd of Virginia.

Another accident offered Tyson his opportunity to pioneer on the perilous paths of human origins. An infant chimpanzee which a sailor had loaded on his ship in Angola in southwest Africa had suffered en route an injury that became infected, and it died soon after its arrival in London. Tyson, who had seen the animal while it was still alive, secured the body, and took it to his house for dissection. Lacking refrigeration for his specimen, Tyson had to perform his dissection speedily. By good luck he enlisted as his assistant one of the ablest human anatomists of the day, William Cowper, who helped him make drawings. Their product, published in 1699, was *Orang-Outang, sive Homo Sylvestris: or, the Anatomy of a Pygmie compared with that of a Monkey, an Ape, and a Man.* Just as Vesalius' book had opened human anatomy, this copiously illustrated volume of some 165 pages opened a new era in physical anthropology.

The term "orang-outang," in the Malay language, meant "man of the woods" and in Europe was then being used loosely for all the larger nonhuman primates. The animal that Tyson dissected was not what the modern zoologist would call an orang-outang but an African chimpanzee. This animal, the first anthropoid to appear in European scientific literature, had been noted in 1641 by Dr. Nicolaes Tulp (whom Rembrandt depicted as the teacher in his famous *Anatomy Lesson*). Tyson chose to call his specimen a "pygmie."

What he called it was less important than what he did with it, which was epoch-making. Tyson's anatomy of the orang-outang placed man in a whole new constellation. Just as Copernicus displaced the earth from the center of the universe, so Tyson removed man from his unique role above and apart from all the rest of Creation, for whose nutriment, clothing, and delight plants were created, and for whose service there was a world of animals. Never before had there been so circumstantial or so public a demonstration of man's physical kinship with the animals. Just as Vesalius had detailed and drawn the structure of the human body, so Tyson now detailed the anatomy of what he showed to be man's closest relative among the animals. The implication was plain that here was the "missing link" between man and the whole "lower" animal creation.

Tyson starkly enumerated physical similarities and differences between the chimpanzee and man. Without references to God or speculations about an immortal soul, he listed his conclusions in two columns. One itemized how "The Orang-Outang or Pygmie more resembled a Man, than Apes and Monkeys do," another how it "differ'd from a Man, and resembled more the Ape and Monkey-kind." The forty-eight items of resemblance to man began with "1. In having the Hair of the Shoulder tending downwards; and that of the Arm, upwards," and went through the structural similarities of intestines, colon, liver, spleen, pancreas, and heart. "25. The Brain was abundantly larger than in Apes; and all it's Parts exactly formed like the Humane Brain." Then similarities of teeth, vertebrae, fingers and toes, but finally "whether all the same Muscles in Apes and Monkeys resemble the Humane, could not be determined, for want of a Subject to compare them with, or Observations made by others." The thirty-four anatomical differences from man, and the chimpanzee's resemblances "to the Ape and Monkey-kind" were also listed with technical precision. Having found that the organs of speech and the brain of his pygmie "does so exactly resemble a Man's," he left his readers to puzzle "that there is no reason to think that Agents do perform such and such Actions, because they are found with Organs proper thereunto: for then our Pygmie might be really a Man." Why could man reason, while pygmies could not? Tyson put this question in a new matrix, in the world of physical nature. Just as the heliocentric vista once seen could not be forgotten, so, after reading Tyson, who could believe that man was an isolate from the rest of nature?

Tyson concluded that the chimpanzee more closely resembled man than it resembled the other primates. Man's differences from other animals now became only matters of nuance to be set down on a list. Tyson's expert dissection gave to the theologians' talk of man's "animal" nature a newly precise—and theologically dangerous—meaning. Tyson was on the threshold of physical anthropology.

In the appendix to his *Orang-Outang* he marshaled his copious classical learning to explain how this creature had stimulated reports of satyrs, of men with dog's heads, and of sphinxes—but "they were only a Creature of the Brain, produced by a warm and wanton Imägination, and . . . they never had any Existence or Habitation elsewhere." So he opened the way, too, to cultural anthropology, showing how different peoples gave wild and varied meanings to the same physical phenomenon, to a mere chimpanzee.

Most surprising in the career of so emphatically *physical* an anthropologist was Tyson's pioneer role in treating the vagaries of the human mind. On his way to become the leading English physician of the age, he was elected a Fellow of the Royal College of Physicians, and in 1684 he was named Physician and then Governor to the Bethlehem Hospital. There he

earned a place in the pantheon of humanitarians. Bethlehem Hospital, founded in the thirteenth century as a priory for the Order of the Star of Bethlehem, became an asylum for the insane, the first such institution in England. Except for one in Granada, Spain, it was also the first in Europe. When Tyson took charge, "Bedlam" (a common pronunciation of Bethlehem) had long since entered common parlance to mean any place of noise and confusion. There the mentally ill were beaten, shackled, and confined in cells. Bedlam had become so public a spectacle that a staple scene in Restoration comedies showed fashionable people "going to see the Lunatics," as if they were a circus or a zoo. And incidentally, Bedlam was a place of assignation for "lewd or disorderly" persons and for lazy apprentices.

Governors of Bedlam had been reluctant to exclude sightseers, since wealthy "idlers" sometimes took an interest in the institution and made contributions. "'Tis by the help of such Benefactors," Tyson himself conceded, "that this Hospital is enabled to bear their great Charges." He tried at least to restrict spectators to the more respectable and prohibited all tourists on Sundays.

In a callous age, Tyson was remarkably successful in humanizing treatment of the mentally ill. To change the atmosphere of a jail into that of a hospital, he brought in women nurses, and set up a wardrobe fund to clothe poor patients. "Bedlam" began to become a place not for punishment but for therapy. His great innovation was the postinstitutional treatment of discharged patients, with periodic visits to them at home. During the twenty years that he was the Physician, of 1,294 patients admitted, 890, or some 70 percent, were discharged with their madness cured or relieved. Tyson's reforms survived the centuries and left a permanent mark at Bethlehem and elsewhere. In 1708 the threnodist wrote on his death:

> Great Tyson's Power new Organs cou'd dispense. . . .
> Here ev'n the mental Deprivation cur'd,
> The Man refounded, Light to Souls restor'd,
> The Tyson Art in this Great Cause bestow'd
> Rebuilds ev'n the faln Image of the God.

When Linnaeus later came to place man in his *System of Nature* in 1735, he did not avoid the issue by calling him a fallen angel. Like Tyson, he confessed that he "could not discover the difference between man and the orangutan," and he never did find a single "generic character" to distinguish man from the ape. "It is remarkable," Linnaeus concluded in his twelfth edition, with an irony rare for him, "that the stupidest ape differs so little from the wisest man, that the surveyor of nature has yet to be found who can draw the line between them." "*Homo,*" Shakespeare had said in

Henry IV, Part I, "is a common name to all men." Linnaeus christened man into his binomial system as *Homo sapiens.* He gave *homo* vast new meaning, taking his boldest step when he classified man as a "species," simply another kind of animal. Under Mammalia in his Order of Primates ("Fore-teeth cutting; upper 4, parallel; teats 2 pectoral") Linnaeus placed the human species ("Diurnal; varying by education and situation"), and distinguished these varieties:

> Four-footed, mute, hairy. *Wild Man.*
>
> Copper-coloured, Choleric, erect. *American.*
> Hair black, straight, thick; nostrils wide, face harsh; beard scanty; obstinate, content free. Paints himself with fine red lines. Regulated by customs.
>
> Fair, sanguine, brawny. *Europeans.*
> Hair yellow, brown, flowing; eyes blue; gentle, acute, inventive. Covered with close vestments. Governed by laws.
>
> Sooty, melancholy, rigid. *Asiatic.*
> Hair black; eyes dark; severe, haughty, covetous. Covered with loose garments. Governed by opinions.
>
> Black, phlegmatic, relaxed. *African.*
> Hair black, frizzled; skin silky; nose flat; lips tumid; crafty, indolent, negligent. Anoints himself with grease. Governed by caprice.

59

Paths to Evolution

"THE year which has passed," Thomas Bell, eminent president of the Linnean Society of London reported at the end of 1858, "has not, indeed, been marked by any of those striking discoveries which at once revolutionize . . . the department of science on which they bear; it is only at remote intervals that we can reasonably expect any sudden and brilliant innovation." The select Linnean Society (of which Joseph Banks was a founder) had been created in 1788 to preserve the library, herbarium, and manuscripts which Linnaeus had left to his son, and which on his son's death had been bought for them by an English botanist. Despite Bell's observation, the

three papers read to the society on July 1 of that year bore more revolutionary implications than any other offerings to the forum of scientists since Sir Isaac Newton's day.

Those papers (which came to only seventeen pages in the society's *Journal*), "On the Tendency of Species to form Varieties; and on the Perpetuation of Varieties and Species by Natural Means of Selection," had been communicated to the society by two of its most accomplished fellows, Sir Charles Lyell, the geologist, and J. D. Hooker, the botanist. The sponsors offered "the results of the investigations of two indefatigable naturalists, Mr. Charles Darwin and Mr. Alfred Wallace. These gentlemen having, independently and unknown to one another, conceived the same very ingenious theory to account for the appearance and perpetuation of varieties and of specific forms on our planet, may both fairly claim the merit of being original thinkers in this important line of inquiry." The three items were: extracts from a manuscript sketched by Darwin in 1839 and revised in 1844; the abstract of a letter from Darwin to Professor Asa Gray of Boston, Massachusetts, in October 1857, repeating his views on species stated in the earlier manuscript; and an essay by Wallace written at Ternate in the East Indies in February 1858, which he had sent to Darwin with instructions to forward it to Lyell if he found it sufficiently novel and interesting.

In later years historians would note July 1, 1858, as the date of the first public statement of the modern theory of evolution. But at the time the Darwin-Wallace papers made hardly a ripple. Neither Darwin nor Wallace was present, and there was no discussion by the thirty fellows who were there. A scheduled paper with a contradictory thesis was not even given. The reading of these articles was a rite of priority, required by the new etiquette of science.

In the progress of the idea of evolution we witness a distinctly modern phenomenon in the progress of science. Modern times brought new instruments of publicity, the printing press with its new powers of diffusion, scientific societies with their wider and more public forums. All this meant a new mobility for scientific ideas and for scientists themselves. Of course, the new incrementalism of science did not spell an end to revolutions in thought, but it did change the pace and the character of these revolutions. Now novel ideas could be introduced piecemeal, unobtrusively, even perfunctorily. And who could tell when one of these ideas might signal a revolution in thought? On that July day in London the Linnean Society prepared to publish observations made by Darwin twenty years earlier on his round-the-world voyage on the *Beagle* alongside complementary observations made by Wallace a few months before in Ternate in the distant Moluccas.

When Darwin, a young man of twenty-two, had sailed out on December

27, 1831, on the five-year voyage of the *Beagle*, he took with him the just published first volume of Charles Lyell's *Principles of Geology*, a going-away gift from his Cambridge professor of botany. Lyell (1797–1875) would provide the background for all Darwin's thinking about the processes of nature and so make it possible for modern evolutionary thought to bear the name of Darwinism. Lyell's crucial insight, documented with copious evidence in his book, was that the earth had been shaped from the beginning by uniform forces still at work—erosion by running water, accumulation of sediment, earthquakes, and volcanoes. Since such forces through millennia had made the earth what it was in his day, there was no need to imagine catastrophes. This doctrine, christened by the English philosopher William Whewell, came to be known as Uniformitarianism.

Lyell had tried to avoid the shoals of theology and cosmology simply by refusing to discuss the origins of the earth. Speculative theories of a Creation, he said, were unnecessary and unscientific. The implications for plants and animals were obvious. If the present activity of Vesuvius or Etna explained changes in the surface of the earth, could not other forces equally visible today show us how species and varieties of plants and animals had come into being? The Cambridge professor of botany who gave Darwin the copy of Lyell which he read and cherished on the *Beagle* warned him not to believe everything in it. The few other books he took along included the Bible, Milton, and Alexander von Humboldt's travels in Venezuela and the Orinoco basin.

In the mystery story of how Darwin came to his notions of evolution, the voyage of the *Beagle* was, of course, a crucial episode. An essential link in the chain of people and ideas was John Stevens Henslow (1796–1861), the teacher who first inspired the young Darwin with enthusiasm for the study of nature. From the chair of botany the handsome magnetic Henslow single-handedly stirred a botanical renaissance in the university. He initiated field trips to observe plants in their natural habitat and required his students to make independent observations, training a new generation of botanists interested less in Linnaean taxonomy than in plant distribution, ecology, and geography. The Cambridge Botanical Garden became a teaching laboratory.

Henslow's historic accomplishment was to transform the Cambridge playboy Darwin from a listless student of theology into a passionate naturalist. At the age of sixty-seven, Darwin still recalled "a circumstance which influenced my career more than any other":

> This was my friendship with Prof. Henslow. Before coming up to Cambridge, I had heard of him from my brother as a man who knew every branch of science, and I was accordingly prepared to reverence him. He kept open house once every

> week, where all undergraduates and several older members of the University, who were attached to science, used to meet in the evening. I soon got through Fox an invitation and went there regularly. Before long I became well acquainted with Henslow, and during the latter half of my time at Cambridge took long walks with him on most days; so that I was called by some of the dons "the man who walks with Henslow"; and in the evening I was very often asked to join his family dinner. His knowledge was great in botany, entomology, chemistry, mineralogy and geology. His strongest taste was to draw conclusions from long-continued minute observations.

In 1831, when the Admiralty asked Henslow to recommend a naturalist to serve on the *Beagle*'s voyage to map the coasts of Patagonia, Tierra del Fuego, Chile, and Peru and to set up chronometric stations, he recommended his favorite pupil.

Charles was eager to accept. But his father, already irritated by Charles' false start at Edinburgh in the study of medicine, was dead set against any more such casual adventures. "You care for nothing but shooting, dogs, and rat-catching," the elder Darwin had complained, "and you will be a disgrace to yourself and all your family." Now he was determined to keep the vagrant Charles on the path to the clergy, and the dutiful son would not join the *Beagle* without his father's permission. Luckily, Professor Henslow and Charles' uncle, Josiah Wedgwood II, succeeded in persuading Charles' father to let Charles go. "The pursuit of Natural History," Wedgwood argued, "though certainly not professional, is very suitable to a clergyman."

Henslow kept in close touch with his pupil during the five-year voyage of the *Beagle*. They corresponded regularly, and Henslow looked after the specimens that Darwin sent back to London. When the *Beagle* arrived at Montevideo a copy of Lyell's second volume was awaiting, and at Valparaiso on the other side of the South American continent Darwin received the third volume, just off the press. Throughout his trip Darwin was applying Lyell's principles. And at the coral-encrusted rims of submerged volcanic craters in the Indian Ocean, he concluded that the Kelling Atoll had been built up over at least a million years.

The second volume of Lyell went beyond physical geology and applied his Uniformitarianism to biology. Throughout geological time, Lyell explained, new species had been emerging, and others had become extinct. Survival of a species depended on certain conditions of its environment, but geological processes were constantly changing those conditions. Failure in competition with other species in the same habitat might extinguish a species. The success of one prosperous species might crowd out others to extinction. Lyell's survey of the geographic distribution of plants and animals suggested that each species had come into being in one center. Similar habitats on separate continents seemed to produce quite different species

equally adapted to their habitats. Environment, species—everything was in flux.

Lyell's interest in these problems had been piqued by the French naturalist Lamarck (1744–1829). But Lamarck, insisting on the inheritance of acquired characteristics, had really abandoned the concept of species. For him a species was only a name for one set of generations while the animal was adapting to its environment. And if every species was infinitely plastic, then no species would ever have to become extinct. While Lyell had kept species as the essential units in his processes of nature, he could not explain how a new species would originate.

The impressionable Darwin was tantalized by Lyell's suggestions. Everywhere in South America he encountered plants and animals he had never seen before. In the Galápagos he was enticed by the variations of bird species on widely separated islands in the same latitude. Meanwhile, Henslow had been so much impressed by Darwin's letters that he had read some of them to the Philosophical Society of Cambridge, and even printed some of them for private distribution. When the *Beagle* returned in 1836, Henslow joined with Lyell in securing for Darwin a grant of £1,000 to help him compile his five-volume report, and then managed his election as Secretary of the Geological Society of London.

During the next few years Darwin, by his own account, saw more of Lyell than of any other man. "His delight in science was ardent," Darwin recalled, "and he felt the keenest interest in the future progress of mankind. He was very kind-hearted, and thoroughly liberal in his beliefs or rather disbeliefs." Still Lyell would be slow in coming around to Darwin's own theories. "What a good thing it would be," the young Darwin had complained to Lyell when older geologists refused to follow Lyell, "if every scientific man was to die when 60 years old, as afterwards he would be sure to oppose all new doctrines." But in his late sixties the courageous Lyell's *Antiquity of Man* (1863) would finally abandon his opposition to evolution and begin to embrace Darwin's views of the origin of species. "Considering his age, his former views, and position in society," observed Darwin, "I think his action has been heroic."

Lyell, twelve years Darwin's senior, and at the height of his fame, remained Darwin's mentor. After the Darwins moved to Down in Kent, the Lyells would come visit for days at a time. As Darwin recalled:

> It appeared to me that by following the example of Lyell in Geology, and by collecting all facts which bore in any way on the variation of animals and plants under domestication and nature, some light might perhaps be thrown on the whole subject. My first note-book was opened in July 1837. I worked on true Baconian principles, and without any theory collected facts on a whole-sale

> scale, more especially with respect to domesticated productions, by printed enquiries, by conversation with skilful breeders and gardeners, and by extensive reading. When I see the list of books of all kinds which I read and abstracted, including whole series of Journals and Transactions, I am surprised at my industry. I soon perceived that Selection was the key-stone of man's success in making useful races of animals and plants. But how selection could be applied to organisms living in a state of nature remained for some time a mystery to me. In October 1838, that is fifteen months after I had begun my systematic enquiry, I happened to read for amusement "Malthus on Population," and being well prepared to appreciate the struggle for existence which everywhere goes on from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved and unfavourable ones to be destroyed. The result of this would be the formation of new species.

Here in a nutshell was what Darwin had to add to the thinking about species.

Still, Darwin was "so anxious to avoid prejudice" from the premature exposure of his ideas, that he held back. In June 1842, for his own satisfaction, he penciled a brief abstract of his theory in 35 pages, which he then enlarged in 1844 to another "abstract" of 230 pages. In 1856, when Lyell advised Darwin to expand his treatment, he began at once "to do so on a scale three or four times as extensive as that which was afterwards followed in my Origin of Species."

Then, early in the summer of 1858, as Darwin recorded, all his "plans were overthrown." He received from the Moluccas Wallace's essay "on the tendency of varieties to depart indefinitely from the original type." Wallace asked him, if he thought well of the essay, to send it on to Lyell, and, as we have seen, the scrupulous Darwin did just that. If Wallace's paper was to be published, what would Darwin do with his own labored product of twenty years? Darwin was torn.

Again Lyell, the statesman in the new parliament of science, played a crucial role. Determined to preserve Darwin's claim to priority and at the same time to give Wallace his due, Lyell urged that the three items be promptly offered to the Linnean Society. "I was at first very unwilling to consent," Darwin confessed, "as I thought Mr. Wallace might consider my doing so unjustifiable, for I did not then know how generous and noble was his disposition. The extract from my M.S and the letter to Asa Gray had neither been intended for publication and were badly written. Mr. Wallace's essay, on the other hand was admirably expressed and quite clear. Nevertheless our joint productions excited very little attention, and the only published notice of them which I can remember was by Prof. Haughton of

Dublin, whose verdict was that all that was new in them was false, and what was true was old."

Alfred Russel Wallace (1823–1913), whom history would recognize as co-author of the idea of natural selection, offered a vivid contrast to Darwin. Born into an impoverished family of nine children in Monmouthshire in South Wales, he attended a grammar school for a few years, dropped out at fourteen, and educated himself by reading. As a boy visiting London he frequented the "Hall of Science" in Tottenham Court Road, a workmen's club for advanced teachers where he was converted to Robert Owen's socialism and "secularism," a skepticism of all religions. He supported himself as an apprentice-surveyor with his brother, then read up enough on his own to qualify as a schoolmaster in Leicester. There he had the good luck to meet Henry Walter Bates (1825–1892), who had been working thirteen hours a day drearily apprenticed to a local hosiery manufacturer, but was finding his refuge in Homer, Gibbon, and amateur entomology. Bates and Wallace became fast friends, and joined in beetle-collecting expeditions into the countryside.

A voracious reader, the young Wallace discovered an inspiring assortment of books on science, natural history, and travel, including Malthus' *On Population,* Darwin's journal of the *Beagle,* and Lyell's *Geology.* One of the books that impressed him most was a stimulating book on evolution by another amateur naturalist, Robert Chambers (1802–1871). *Vestiges of the Natural History of Creation* (1844) was so controversial that Chambers had to publish it anonymously to avoid damage to his publishing business, but it went through four editions in seven months and soon sold twenty-four thousand copies. Though condemned as godless by respectable scientists, it irrevocably popularized the ideas of organic and cosmic evolution, and the evolution of species.

Alexander von Humboldt's dramatic personal account of his travels in Mexico and South America emboldened Wallace to enlist Bates on an expedition to gather specimens along the Amazon. Four years (1848–52) of collecting there earned young Wallace a reputation as a field naturalist. On his return voyage to England his ship caught fire and sank, along with his specimens, but he was not discouraged from collecting. He set out promptly for the Malay Archipelago. There and in the Moluccas he spent eight years exploring and gathering specimens, and formulated the theory of natural selection in the paper that Darwin received early in 1858.

If a Greek dramatist had contrived two characters to show how fate could bring men by opposite paths to the same destination, he could hardly have done better than invent Darwin and Wallace. Darwin, the elder by a dozen years, had been dedicated by his wealthy family to a career in the Church. All his life Darwin did his best to follow Lyell's advice "never to get

entangled in a controversy, as it rarely did any good and caused a miserable loss of time and temper." Tediously gathering specimens and evidence over two decades, Darwin seemed led to his theory of natural selection almost against his will. The impoverished Wallace, inspired early with a suspicion of religion and all established institutions, was hasty to embrace theories and plunge into controversy. When he was only twenty-two, Chambers' popular *Vestiges* had converted Wallace to an unshakable conviction that species arose through a process of evolution, and his trip to the Amazon was for facts to convince others. By his later trip through the Malay Archipelago covering fifteen thousand miles and gathering some 127,000 specimens, he aimed to gather conclusive evidence. From his arrival there he kept a notebook on evolution, which he called his "Species Notebook." Wallace's essay "On the Law which Has Regulated the Introduction of New Species" (1855) was published three years before the paper he sent to Darwin.

During the 1860's, the very years when the elementary notions of evolution were being publicly tested, Wallace spread himself over the most miscellaneous causes. He became a passionate convert to Spiritualism, pursuing his interest in socialism he was elected the first president of the Land Nationalization Society (1881), and he was an outspoken advocate of women's rights. Curiously, his passion for controversy drew him into the movement against vaccination for smallpox. His pamphlet *Forty-five Years of Registration Statistics, Proving Vaccination to Be Both Useless and Dangerous* (1885) was followed by three days of testimony before the Royal Commission where he argued that more patients died from vaccination than from the disease.

Seeking a wider arena for controversy, Wallace reached into outer space. The eminent astronomer Percival Lowell (1855–1916) argued in *Mars and Its Canals* (1906) that there must have been intelligent inhabitants on Mars, who had made the channels now visible by building a system of irrigation —using water from the annually melting polar ice caps—which created bands of cultivated vegetation. Wallace, though no astronomer, at the age of eighty-four entered the lists. In *Is Mars Habitable?* (1907) he insisted that life could not exist elsewhere in the universe. And twentieth-century evidence has proved that the expert Lowell was probably farther from the truth than the amateur Wallace. Science and reform had produced what Wallace enthusiastically christened *The Wonderful Century* (1898).

The facts of geographical distribution that provided the cautious Darwin with questions supplied the brash Wallace with answers. Seeing natural selection led Darwin away from religious faith. Late in life he recalled that the grandeur of the Brazilian forest had once reinforced his "firm conviction of the existence of God and of the immortality of the soul. . . . But now the

grandest scenes would not cause any such convictions and feelings to rise in my mind. It may be truly said that I am like a man who has become colour-blind." "There seems to be no more design to the variability of organic beings and in the action of natural selection, than in the course which the wind blows."

But Wallace's passion for evolution led him more and more toward a belief in a "Higher Intelligence." Increasingly he needed a God to explain what he saw in nature. "I hope," Darwin told Wallace when Wallace's review of Lyell's books in 1869 laid bare his resurgent faith in a God, "you have not murdered too completely your own and my child."

Just as the voyages of Gama and Magellan had been preceded by uncelebrated pioneers on trading voyages across the Mediterranean and by those who inched down around the coast of Africa, so too there were countless pioneers in the voyages toward evolution. But while Columbus knew there was a Japan to be reached, Gama that India was there, the pioneers of evolution were en route to an unknown destination.

To describe amply all who contributed to Darwin's mature theory of evolution would require volumes on the rise of modern biology, geology, and geography. We would have to recount ancient Greek foreshadowings, Saint Augustine's suggestion that while all species had been created by God in the Beginning, some were mere seeds that would appear at a later time, medieval notions of an organic world, Montesquieu's hints of the multiplication of species from the discovery in Java of flying lemurs, the French mathematician Maupertuis's speculations on the chance combinations of elementary particles, Diderot's suggestions that higher animals may all have descended from "one primeval animal," Buffon on the development and "degeneration" of species, Linnaeus' gnawing doubts that species might not be immutable, the metaphoric fancies of Charles' grandfather Erasmus Darwin on the urges of plants and animals sparked by "lust, hunger, and danger" to develop into new forms—and countless others.

Among earlier contemporaries of Darwin we would have to include Lamarck's bold exploration of the hazy borderland between species and varieties and his evolutionary "tree." Nor could we omit Georges Cuvier's grand systematic arrangement of all classes of the animal kingdom. "These diverse bodies may be looked upon as a kind of experiment performed by nature," Cuvier ventured in 1817, "which adds or subtracts from each of these different parts (just as we try to do the same in our laboratories) and itself shows the results of these additions and subtractions." Many others who, like Cuvier, denied the evolution of species, still detected progress in the sorts of creatures found in the more recent levels of the earth.

Cuvier's *bête noire,* the indomitable Etienne Geoffroy Saint-Hilaire

(1772–1844), took up Napoleon's invitation to join the scientific expedition to Egypt and at the risk of his life collected specimens from the tombs. He translated "evolution" from a word for the embryonic development of the individual into a word for the emergence of species. For Geoffroy, the structural similarity of all vertebrates suggested the evolution of mammals from fishes, and he declared the evolution of the whole animal kingdom. But he said that the innovator, like Christ, must be willing to wear a crown of thorns.

The data for evolution were an unanticipated by-product of a seafaring expedition which had a clearly defined assignment. The *Beagle,* as we have seen, had been sent by the British Admiralty to chart the coast of South America and to fix longitude more accurately by a world-encircling chain of chronological calculations. But the modern parliaments of science—the Royal Society, the Linnean Society, and their counterparts across Europe and the Americas—had made natural history a deliberate forum for the unexpected.

The triumph of evolution was a victory not merely of ideas but of printed matter, which in its European typographic form was a revolutionary new device for spreading grand ideas to the most unlikely places. *An Essay on the Principle of Population* (1798), by Thomas Robert Malthus (1766–1834), which Darwin had read in October 1838, would also catalyze Wallace. In his *Autobiography,* Wallace recalled that when he was a schoolteacher in Leicester in 1844–45 passing many hours in the town library, "perhaps the most important book I read was Malthus's 'Principles of Population,' which I greatly admired for its masterly summary of facts and logical induction to conclusions. It was the first work I had yet read treating any of the problems of philosophical biology, and its main principles remained with me as a permanent possession and twenty years later gave me the long-sought clue to the effective agent in the evolution of organic species." And he recorded vividly the moment when Malthus reappeared on his horizon and changed his life. In January 1858 Wallace had just arrived at Ternate in the Moluccas to collect butterflies and beetles, "bitten by the passion for species and their description, and if neither Darwin nor myself had hit upon 'Natural Selection,' I might have spent the best years of my life in this comparatively profitless work." His thinking had reached a dead end.

> I was suffering from a sharp attack of intermittent fever, and every day during the cold and succeeding hot fits had to lie down for several hours, during which time I had nothing to do but to think over any subjects then particularly interesting me. One day something brought to my recollection Malthus's "Principles of Population," which I had read twelve years before. I thought of his clear exposition of "the positive checks to increase"—disease, accidents, war, and famine—

> which keep down the population of savage races to so much lower an average than that of more civilized peoples. It then occurred to me that these causes or their equivalents are continually acting in the case of animals also; and as animals usually breed much more rapidly than does mankind, the destruction every year from these causes must be enormous in order to keep down the numbers of each species . . . as otherwise the world would long ago have been densely crowded with those that breed most quickly. . . . Why do some die and some live? And the answer was clearly, that on the whole the best fitted live. From the effects of disease the most healthy escaped; from enemies, the strongest, the swiftest, or the most cunning; from famine, the best hunters or those with the best digestion; and so on. Then it suddenly flashed upon me that this self-acting process would necessarily *improve the race,* because in every generation the inferior would inevitably be killed off and the superior would remain—that is, *the fittest would survive.* . . . I waited anxiously for the termination of my fit so that I might at once make notes for a paper on the subject.

The following two evenings he spent writing the paper that he sent to Darwin by the next post, with the results we have already seen.

Malthus' ideas on population had been a reaction against his father's admiration for the utopian ideas of Rousseau and William Godwin. Though destined for the clergy and actually ordained, the young Malthus at Cambridge had done brilliantly in mathematics. "Population, when unchecked," he gave as the heart of his "principle," "increases in a geometrical ratio. Subsistence increases only in arithmetical ratio." And despite his frequent old-fashioned moralizing, his book had the ring of quantitative social science. Malthus had an eminently practical purpose—to reshape the Poor Laws so that the leaders of England "would not be open to the objection of violating our promises to the poor." And in the long run he would influence economic thinking. Karl Marx learned from him, and John Maynard Keynes would credit Malthus with the idea that effective demand was a way of avoiding depressions. But Malthus' influence on biology was quite unpredicted. The struggle for existence, Darwin explained in the *Origin of Species,* "is the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdom." The cogency of Malthus' style had much to do with the remarkable impact of his small book, which went through six editions before his death and increased in power with the years.

Publication was often the crux of the matter. Whether readers agreed or disagreed, what mattered was that the published book sparked discussion as it sold copies. When Darwin's *Origin of Species* was offered to the shrewd John Murray (who had published a revised *Voyage of the Beagle* and Herman Melville's tales of the South Seas after several others had refused), he was far from enthusiastic. The cautious Darwin asked Lyell on March 28, 1859, how he should approach Murray:

> P.S. Would you advise me to tell Murray that my book is not more *un*-orthodox than the subject makes inevitable. That I do not discuss the origin of man. That I do not bring in any discussion about Genesis, &c., &c., and only give facts, and such conclusions from them as seem to me fair.
>
> Or had I better say *nothing* to Murray, and assume that he cannot object to this much unorthodoxy, which in fact is not more than any Geological Treatise which runs slap counter to Genesis.

Finally, all that Murray objected to were the words "Abstract" and "Natural Selection" in the title. Seeing only the chapter titles, and on Lyell's recommendation, Murray agreed to publish, giving Darwin two-thirds of the net profit.

The Reverend Whitwell Elwin, editor of the prestigious *Quarterly Review,* in a reader's report, which would become a classic in the trade, advised Murray that it was unwise to publish anything that called itself only an "abstract." Since the subject was so controversial, Elwin urged that, instead, Darwin should write a book on pigeons, on which he was known to have some ingenious observations. "Everyone is interested in pigeons," he added. "The book would be reviewed in every journal in the kingdom and would soon be on every library table." Darwin was not persuaded.

A lawyer friend of Murray's encouraged him to print 1,000 copies instead of the planned 500, and the number was raised to 1,250 before publication on November 24, 1859. Until the last moment Darwin feared that Murray was overcommitted, and even offered to pay the cost of his proof corrections. When all copies were taken by booksellers, another 3,000 were printed. The result was beyond expectations. "Sixteen thousand copies have now (1876) been sold in England," Darwin noted in his *Autobiography,* "and considering how stiff a book it is this is a large sale. It has been translated into almost every European tongue, even into such languages as Spanish, Bohemian, Polish, and Russian. It has also, according to Miss Bird, been translated into Japanese and is there much studied. Even an essay in Hebrew has appeared on it, showing that the theory is contained in the Old Testament!" He proudly counted more than 265 reviews, and numerous essays. Darwin attributed the publishing success (not large, for popular novels were equaling Darwin's boasted total in a single year) to his bringing together "innumerable well-observed facts," and to the moderate size of the book, which he said he owed to help from Wallace's essay.

The initial hostile reception of the *Origin of Species,* and especially the ignorant and contemptuous attack by Bishop Samuel Wilberforce, has become proverbial. But contempt rapidly gave way to acclaim. Within a decade of publication, questions for the natural science tripos at Cambridge, instead of asking for "evidence of design" in nature, required an analysis

of the concept of the struggle for existence. When even the ill-tempered Bishop Wilberforce reluctantly confessed his error, Darwin's champion, Thomas Henry Huxley, remained unsatisfied. "Confession unaccompanied by penitence . . . affords no ground for mitigation of judgment; and the kindliness with which Mr. Darwin speaks of his assailant, Bishop Wilberforce, is so striking an exemplification of his singular gentleness and modesty, that it rather increases one's indignation against the presumption of his critic." Huxley called Darwin's book "the most potent instrument for the extension of the realm of natural knowledge which has come into men's hands, since the publication of Newton's Principia." "It was badly received by the generation to which it was first addressed, and the outpouring of angry nonsense to which it gave rise is sad to think upon. But the present generation will probably behave just as badly if another Darwin should arise, and inflict upon them what the generality of mankind most hate—the necessity of revising their convictions."

The long-term influence of Darwinism and its fruitful ambivalence for science and religion was embodied in Huxley's invention of the word "agnostic" to describe the limits and the promise of scientific knowledge. Huxley took his clue from Saint Paul's encounter with the Athenians worshipping at an altar inscribed "To the Unknown God." On the urging of twenty members of Parliament, when Darwin died in 1882 he was buried in Westminster Abbey.

PART II

DARWINIAN EVOLUTION

Darwin, Charles: *On the Origin of Species by means of Natural Selection or the Preservation of Favored Races in the Struggle for Life*, edited from the First Edition (Nov. 1859)

Wallace, Alfred. R.: *On the Tendency of Varieties to Depart Indefinitely from the Original Type* (from Chapter 9, *Galileo's Commandment*, edited by E. B. Bolles)

On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life.

By Charles Darwin

[Extracts from the first edition, London, 1859. Pagination does not follow the original pagination.]

Introduction

When on board H.M.S. 'Beagle,' as naturalist, I was much struck with certain facts in the distribution of the inhabitants of South America, and in the geological relations of the present to the past inhabitants of that continent. These facts seemed to me to throw some light on the origin of species–that mystery of mysteries, as it has been called by one of our greatest philosophers. On my return home, it occurred to me, in 1837, that something might perhaps be made out on this question by patiently accumulating and reflecting on all sorts of facts which could possibly have any bearing on it. After five years' work I allowed myself to speculate on the subject, and drew up some short notes; these I enlarged in 1844 into a sketch of the conclusions, which then seemed to me probable: from that period to the present day I have steadily pursued the same object. I hope that I may be excused for entering on these personal details, as I give them to show that I have not been hasty in coming to a decision.

My work is now nearly finished; but as it will take me two or three more years to complete it, and as my health is far from strong, I have been urged to publish this Abstract. I have more especially been induced to do this, as Mr. Wallace, who is now studying the natural history of the Malay Archipelago, has arrived at almost exactly the same general conclusions that I have on the origin of species. Last year he sent to me a memoir on this subject, with a request that I would forward it to Sir Charles Lyell, who sent it to the Linnean Society, and it is published in the third volume of the Journal of that Society. Sir C. Lyell and Dr. Hooker, who both knew of my work–the latter having read my sketch of 1844–honoured me by thinking it advisable to publish, with Mr. Wallace's excellent memoir, some brief extracts from my manuscripts.

This Abstract, which I now publish, must necessarily be imperfect. I cannot here give references and authorities for my several statements; and I must trust to the reader reposing some confidence in my accuracy. No doubt errors will have crept in, though I hope I have always been cautious in trusting to good authorities alone. I can here give only the general conclusions at which I have arrived, with a few facts in illustration, but which, I hope, in most cases will suffice. No one can feel more sensible than I do of the necessity of hereafter publishing in detail all the facts, with references, on which my conclusions have been grounded; and I hope in a future work to do this. For I am well aware that scarcely a single point is discussed in this volume on which facts cannot be adduced, often apparently leading to conclusions directly opposite to those at which I have arrived. A fair result can be obtained only by fully stating and balancing the facts and arguments on both sides of each question; and this cannot possibly be here done.

I much regret that want of space prevents my having the satisfaction of acknowledging the generous assistance which I have received from very many naturalists, some of them personally unknown to me. I cannot, however, let this opportunity pass without expressing my deep obligations to Dr. Hooker, who for the last fifteen years has aided me in every possible way by his large stores of knowledge and his excellent judgment.

In considering the Origin of Species, it is quite conceivable that a naturalist, reflecting on the mutual affinities of organic beings, on their embryological relations, their geographical distribution, geological succession, and other such facts, might come to the conclusion that each species had not been independently created, but had descended, like varieties, from other species. Nevertheless, such a conclusion, even if well founded, would be unsatisfactory, until it could be shown how the innumerable species inhabiting this world have been modified, so as to acquire that perfection of structure and coadaptation which most justly excites our admiration. Naturalists continually refer to external conditions, such as climate, food, &c., as the only possible cause of variation. In one very limited sense, as we shall hereafter see, this may be true; but it is preposterous to attribute to mere external conditions, the structure, for instance, of the woodpecker, with its feet, tail, beak, and tongue, so admirably adapted to catch insects under the bark of trees. In the case of the misseltoe, which draws its nourishment from certain trees, which has seeds that must be transported by certain birds, and which has flowers with separate sexes absolutely requiring the agency of certain insects to bring pollen from one flower to the other, it is equally preposterous to account for the structure of this parasite, with its relations to several distinct organic beings, by the effects of external conditions, or of habit, or of the volition of the plant itself.

The author of the 'Vestiges of Creation' would, I presume, say that, after a certain unknown number of generations, some bird had given birth to a woodpecker, and some plant to the misseltoe, and that these had been produced perfect as we now see them; but this assumption seems to me to be no explanation, for it leaves the case of the coadaptations of organic beings to each other and to their physical conditions of life, untouched and unexplained.

It is, therefore, of the highest importance to gain a clear insight into the means of modification and coadaptation. At the commencement of my observations it seemed to me probable that a careful study of domesticated animals and of cultivated plants would offer the best chance of making out this obscure problem. Nor have I been disappointed; in this and in all other perplexing cases I have invariably found that our knowledge, imperfect though it be, of variation under domestication, afforded the best and safest clue. I may venture to express my conviction of the high value of such studies, although they have been very commonly neglected by naturalists.

From these considerations, I shall devote the first chapter of this Abstract to Variation under Domestication. We shall thus see that a large amount of hereditary modification is at least possible, and, what is equally or more important, we shall see how great is the power of man in accumulating by his Selection successive slight variations. I will then pass on to the variability of species in a state of nature; but I shall, unfortunately, be compelled to treat this subject far too briefly, as it can be treated properly only by giving long catalogues of facts. We shall, however, be enabled to discuss what circumstances are most favourable to variation. In the next chapter the Struggle for Existence amongst all organic beings throughout the world, which inevitably follows from their high geometrical powers of increase, will be treated of. This is the doctrine of Malthus, applied to the whole animal and vegetable kingdoms. As many more individuals of each species are born than can possibly survive; and as, consequently, there is a frequently recurring struggle for existence, it follows that any being, if it vary however slightly in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be naturally selected. From the strong principle of inheritance, any selected variety will tend to propagate its new and modified form.

This fundamental subject of Natural Selection will be treated at some length in the fourth chapter; and we shall then see how Natural Selection almost inevitably causes much Extinction of the less improved forms of life and induces what I have called Divergence of Character. In the next chapter I shall discuss the complex and little known laws of variation and of correlation of growth. In the four succeeding chapters, the most apparent and gravest

difficulties on the theory will be given: namely, first, the difficulties of transitions, or in understanding how a simple being or a simple organ can be changed and perfected into a highly developed being or elaborately constructed organ; secondly the subject of Instinct, or the mental powers of animals, thirdly, Hybridism, or the infertility of species and the fertility of varieties when intercrossed; and fourthly, the imperfection of the Geological Record. In the next chapter I shall consider the geological succession of organic beings throughout time; in the eleventh and twelfth, their geographical distribution throughout space; in the thirteenth, their classification or mutual affinities, both when mature and in an embryonic condition. In the last chapter I shall give a brief recapitulation of the whole work, and a few concluding remarks.

No one ought to feel surprise at much remaining as yet unexplained in regard to the origin of species and varieties, if he makes due allowance for our profound ignorance in regard to the mutual relations of all the beings which live around us. Who can explain why one species ranges widely and is very numerous, and why another allied species has a narrow range and is rare? Yet these relations are of the highest importance, for they determine the present welfare, and, as I believe, the future success and modification of every inhabitant of this world. Still less do we know of the mutual relations of the innumerable inhabitants of the world during the many past geological epochs in its history. Although much remains obscure, and will long remain obscure, I can entertain no doubt, after the most deliberate study and dispassionate judgment of which I am capable, that the view which most naturalists entertain, and which I formerly entertained–namely, that each species has been independently created–is erroneous. I am fully convinced that species are not immutable; but that those belonging to what are called the same genera are lineal descendants of some other and generally extinct species, in the same manner as the acknowledged varieties of any one species are the descendants of that species. Furthermore, I am convinced that Natural Selection has been the main but not exclusive means of modification.

Chapter III

Struggle for Existence

Bears on natural selection – The term used in a wide sense – Geometrical powers of increase – Rapid increase of naturalized animals and plants – Nature of the checks to increase – Competition universal – Effects of climate – Protection from the number of individuals – Complex relations of all animals and plants throughout nature – Struggle for life most severe between individuals and varieties of the same species; often severe between species of the same genus – The relation of organism to organism the most important of all relations.

Before entering on the subject of this chapter, I must make a few preliminary remarks, to show how the struggle for existence bears on Natural Selection. It has been seen in the last chapter that amongst organic beings in a state of nature there is some individual variability; indeed I am not aware that this has ever been disputed. It is immaterial for us whether a multitude of doubtful forms be called species or sub-species or varieties; what rank, for instance, the two or three hundred doubtful forms of British plants are entitled to hold, if the existence of any well-marked varieties be admitted. But the mere existence of individual variability and of some few well-marked varieties, though necessary as the foundation for the work, helps us but little in understanding how species arise in nature. How have all those exquisite adaptations of one part of the organisation to another part, and to the conditions of life, and of one distinct organic being to another being, been perfected? We see these beautiful co-adaptations most plainly in the woodpecker and missletoe; and only a little less plainly in the humblest parasite which clings to the hairs of a quadruped or feathers of a bird; in the

structure of the beetle which dives through the water; in the plumed seed which is wafted by the gentlest breeze; in short, we see beautiful adaptations everywhere and in every part of the organic world.

Again, it may be asked, how is it that varieties, which I have called incipient species, become ultimately converted into good and distinct species, which in most cases obviously differ from each other far more than do the varieties of the same species? How do those groups of species, which constitute what are called distinct genera, and which differ from each other more than do the species of the same genus, arise? All these results, as we shall more fully see in the next chapter, follow inevitably from the struggle for life. Owing to this struggle for life, any variation, however slight and from whatever cause proceeding, if it be in any degree profitable to an individual of any species, in its infinitely complex relations to other organic beings and to external nature, will tend to the preservation of that individual, and will generally be inherited by its offspring. The offspring, also, will thus have a better chance of surviving, for, of the many individuals of any species which are periodically born, but a small number can survive. I have called this principle, by which each slight variation, if useful, is preserved, by the term of Natural Selection, in order to mark its relation to man's power of selection. We have seen that man by selection can certainly produce great results, and can adapt organic beings to his own uses, through the accumulation of slight but useful variations, given to him by the hand of Nature. But Natural Selection, as we shall hereafter see, is a power incessantly ready for action, and is as immeasurably superior to man's feeble efforts, as the works of Nature are to those of Art.

We will now discuss in a little more detail the struggle for existence. In my future work this subject shall be treated, as it well deserves, at much greater length. The elder De Candolle and Lyell have largely and philosophically shown that all organic beings are exposed to severe competition. In regard to plants, no one has treated this subject with more spirit and ability than W. Herbert, Dean of Manchester, evidently the result of his great horticultural knowledge. Nothing is easier than to admit in words the truth of the universal struggle for life, or more difficult–at least I have found it so–than constantly to bear this conclusion in mind. Yet unless it be thoroughly engrained in the mind, I am convinced that the whole economy of nature, with every fact on distribution, rarity, abundance, extinction, and variation, will be dimly seen or quite misunderstood. We behold the face of nature bright with gladness, we often see superabundance of food; we do not see, or we forget, that the birds which are idly singing round us mostly live on insects or seeds, and are thus constantly destroying life; or we forget how largely these songsters, or their eggs, or their nestlings, are destroyed by birds and beasts of prey; we do not always bear in mind, that though food may be now superabundant, it is not so at all seasons of each recurring year.

I should premise that I use the term Struggle for Existence in a large and metaphorical sense, including dependence of one being on another, and including (which is more important) not only the life of the individual, but success in leaving progeny. Two canine animals in a time of dearth may be truly said to struggle with each other which shall get food and live. But a plant on the edge of a desert is said to struggle for life against the drought, though more properly it should be said to be dependent on the moisture. A plant which annually produces a thousand seeds, of which on an average only one comes to maturity, may be more truly said to struggle with the plants of the same and other kinds which already clothe the ground. The missletoe is dependent on the apple and a few other trees, but can only in a far-fetched sense be said to struggle with these trees, for if too many of these parasites grow on the same tree, it will languish and die. But several seedling missletoes, growing close together on the same branch, may more truly be said to struggle with each other. As the missletoe is disseminated by birds, its existence depends on birds; and it may metaphorically be said to struggle with other fruit-bearing plants, in order to tempt birds to devour and thus disseminate its seeds

rather than those of other plants. In these several senses, which pass into each other, I use for convenience sake the general term of struggle for existence.

A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase. Every being, which during its natural lifetime produces several eggs or seeds, must suffer destruction during some period of its life, and during some season or occasional year, otherwise, on the principle of geometrical increase, its numbers would quickly become so inordinately great that no country could support the product. Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life. It is the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms; for in this case there can be no artificial increase of food, and no prudential restraint from marriage. Although some species may be now increasing, more or less rapidly, in numbers, all cannot do so, for the world would not hold them.

There is no exception to the rule that every organic being naturally increases at so high a rate, that if not destroyed, the earth would soon be covered by the progeny of a single pair. Even slow-breeding man has doubled in twenty-five years, and at this rate, in a few thousand years, there would literally not be standing room for his progeny. Linnaeus has calculated that if an annual plant produced only two seeds–and there is no plant so unproductive as this–and their seedlings next year produced two, and so on, then in twenty years there would be a million plants. The elephant is reckoned to be the slowest breeder of all known animals, and I have taken some pains to estimate its probable minimum rate of natural increase: it will be under the mark to assume that it breeds when thirty years old, and goes on breeding till ninety years old, bringing forth three pair of young in this interval; if this be so, at the end of the fifth century there would be alive fifteen million elephants, descended from the first pair.

But we have better evidence on this subject than mere theoretical calculations, namely, the numerous recorded cases of the astonishingly rapid increase of various animals in a state of nature, when circumstances have been favourable to them during two or three following seasons. Still more striking is the evidence from our domestic animals of many kinds which have run wild in several parts of the world: if the statements of the rate of increase of slow-breeding cattle and horses in South America, and latterly in Australia, had not been well authenticated, they would have been quite incredible. So it is with plants: cases could be given of introduced plants which have become common throughout whole islands in a period of less than ten years. Several of the plants now most numerous over the wide plains of La Plata, clothing square leagues of surface almost to the exclusion of all other plants, have been introduced from Europe; and there are plants which now range in India, as I hear from Dr. Falconer, from Cape Comorin to the Himalaya, which have been imported from America since its discovery. In such cases, and endless instances could be given, no one supposes that the fertility of these animals or plants has been suddenly and temporarily increased in any sensible degree. The obvious explanation is that the conditions of life have been very favourable, and that there has consequently been less destruction of the old and young, and that nearly all the young have been enabled to breed. In such cases the geometrical ratio of increase, the result of which never fails to be surprising, simply explains the extraordinarily rapid increase and wide diffusion of naturalised productions in their new homes.

In a state of nature almost every plant produces seed, and amongst animals there are very few which do not annually pair. Hence we may confidently assert, that all plants and animals are tending to increase at a geometrical ratio, that all would most rapidly stock every station in which they could any how exist, and that the geometrical tendency to increase must be checked by destruction at some period of life. Our familiarity with the larger domestic animals tends, I think, to mislead us: we see no great destruction falling on them, and we forget that thousands

are annually slaughtered for food, and that in a state of nature an equal number would have somehow to be disposed of.

The only difference between organisms which annually produce eggs or seeds by the thousand, and those which produce extremely few, is, that the slow-breeders would require a few more years to people, under favourable conditions, a whole district, let it be ever so large. The condor lays a couple of eggs and the ostrich a score, and yet in the same country the condor may be the more numerous of the two: the Fulmar petrel lays but one egg, yet it is believed to be the most numerous bird in the world. One fly deposits hundreds of eggs, and another, like the hippobosca, a single one; but this difference does not determine how many individuals of the two species can be supported in a district. A large number of eggs is of some importance to those species, which depend on a rapidly fluctuating amount of food, for it allows them rapidly to increase in number. But the real importance of a large number of eggs or seeds is to make up for much destruction at some period of life; and this period in the great majority of cases is an early one. If an animal can in any way protect its own eggs or young, a small number may be produced, and yet the average stock be fully kept up; but if many eggs or young are destroyed, many must be produced, or the species will become extinct. It would suffice to keep up the full number of a tree, which lived on an average for a thousand years, if a single seed were produced once in a thousand years, supposing that this seed were never destroyed, and could be ensured to germinate in a fitting place. So that in all cases, the average number of any animal or plant depends only indirectly on the number of its eggs or seeds.

In looking at Nature, it is most necessary to keep the foregoing considerations always in mind–never to forget that every single organic being around us may be said to be striving to the utmost to increase in numbers; that each lives by a struggle at some period of its life; that heavy destruction inevitably falls either on the young or old, during each generation or at recurrent intervals. Lighten any check, mitigate the destruction ever so little, and the number of the species will almost instantaneously increase to any amount. The face of Nature may be compared to a yielding surface, with ten thousand sharp wedges packed close together and driven inwards by incessant blows, sometimes one wedge being struck, and then another with greater force. What checks the natural tendency of each species to increase in number is most obscure. Look at the most vigorous species; by as much as it swarms in numbers, by so much will its tendency to increase be still further increased. We know not exactly what the checks are in even one single instance. Nor will this surprise any one who reflects how ignorant we are on this head, even in regard to mankind, so incomparably better known than any other animal. This subject has been ably treated by several authors, and I shall, in my future work, discuss some of the checks at considerable length, more especially in regard to the feral animals of South America. Here I will make only a few remarks, just to recall to the reader's mind some of the chief points. Eggs or very young animals seem generally to suffer most, but this is not invariably the case. With plants there is a vast destruction of seeds, but, from some observations which I have made, I believe that it is the seedlings which suffer most from germinating in ground already thickly stocked with other plants. Seedlings, also, are destroyed in vast numbers by various enemies; for instance, on a piece of ground three feet long and two wide, dug and cleared, and where there could be no choking from other plants, I marked all the seedlings of our native weeds as they came up, and out of the 357 no less than 295 were destroyed, chiefly by slugs and insects. If turf which has long been mown, and the case would be the same with turf closely browsed by quadrupeds, be let to grow, the more vigorous plants gradually kill the less vigorous, though fully grown, plants: thus out of twenty species growing on a little plot of turf (three feet by four) nine species perished from the other species being allowed to grow up freely.

The amount of food for each species of course gives the extreme limit to which each can increase; but very frequently it is not the obtaining food, but the serving as prey to other

animals, which determines the average numbers of a species. Thus, there seems to be little doubt that the stock of partridges, grouse, and hares on any large estate depends chiefly on the destruction of vermin. If not one head of game were shot during the next twenty years in England, and, at the same time, if no vermin were destroyed, there would, in all probability, be less game than at present, although hundreds of thousands of game animals are now annually killed. On the other hand, in some cases, as with the elephant and rhinoceros, none are destroyed by beasts of prey: even the tiger in India most rarely dares to attack a young elephant protected by its dam.

Climate plays an important part in determining the average numbers of a species, and periodical seasons of extreme cold or drought, I believe to be the most effective of all checks. I estimated that the winter of 1854-55 destroyed four-fifths of the birds in my own grounds; and this is a tremendous destruction, when we remember that ten percent is an extraordinarily severe mortality from epidemics with man. The action of climate seems at first sight to be quite independent of the struggle for existence; but in so far as climate chiefly acts in reducing food, it brings on the most severe struggle between the individuals, whether of the same or of distinct species, which subsist on the same kind of food. Even when climate, for instance extreme cold, acts directly, it will be the least vigorous, or those which have got least food through the advancing winter, which will suffer most. When we travel from south to north, or from a damp region to a dry, we invariably see some species gradually getting rarer and rarer, and finally disappearing; and the change of climate being conspicuous, we are tempted to attribute the whole effect to its direct action. But this is a very false view: we forget that each species, even where it most abounds, is constantly suffering enormous destruction at some period of its life, from enemies or from competitors for the same place and food; and if these enemies or competitors be in the least degree favoured by any slight change of climate, they will increase in numbers, and, as each area is already fully stocked with inhabitants, the other species will decrease. When we travel southward and see a species decreasing in numbers, we may feel sure that the cause lies quite as much in other species being favoured, as in this one being hurt. So it is when we travel northward, but in a somewhat lesser degree, for the number of species of all kinds, and therefore of competitors, decreases northwards; hence in going northward, or in ascending a mountain, we far oftener meet with stunted forms, due to the directly injurious action of climate, than we do in proceeding southwards or in descending a mountain. When we reach the Arctic regions, or snow-capped summits, or absolute deserts, the struggle for life is almost exclusively with the elements.

That climate acts in main part indirectly by favouring other species, we may clearly see in the prodigious number of plants in our gardens which can perfectly well endure our climate, but which never become naturalised, for they cannot compete with our native plants, nor resist destruction by our native animals.

When a species, owing to highly favourable circumstances, increases inordinately in numbers in a small tract, epidemics–at least, this seems generally to occur with our game animals–often ensue: and here we have a limiting check independent of the struggle for life. But even some of these so-called epidemics appear to be due to parasitic worms, which have from some cause, possibly in part through facility of diffusion amongst the crowded animals, been disproportionably favoured: and here comes in a sort of struggle between the parasite and its prey.

On the other hand, in many cases, a large stock of individuals of the same species, relatively to the numbers of its enemies, is absolutely necessary for its preservation. Thus we can easily raise plenty of corn and rape-seed, &c., in our fields, because the seeds are in great excess compared with the number of birds which feed on them; nor can the birds, though having a superabundance of food at this one season, increase in number proportionally to the supply of seed, as their numbers are checked during winter: but any one who has tried, knows

how troublesome it is to get seed from a few wheat or other such plants in a garden; I have in this case lost every single seed. This view of the necessity of a large stock of the same species for its preservation, explains, I believe, some singular facts in nature, such as that of very rare plants being sometimes extremely abundant in the few spots where they do occur; and that of some social plants being social, that is, abounding in individuals, even on the extreme confines of their range. For in such cases, we may believe, that a plant could exist only where the conditions of its life were so favourable that many could exist together, and thus save each other from utter destruction. I should add that the good effects of frequent intercrossing, and the ill effects of close interbreeding, probably come into play in some of these cases; but on this intricate subject I will not here enlarge.

Many cases are on record showing how complex and unexpected are the checks and relations between organic beings, which have to struggle together in the same country. I will give only a single instance, which, though a simple one, has interested me. In Staffordshire, on the estate of a relation where I had ample means of investigation, there was a large and extremely barren heath, which had never been touched by the hand of man; but several hundred acres of exactly the same nature had been enclosed twenty-five years previously and planted with Scotch fir. The change in the native vegetation of the planted part of the heath was most remarkable, more than is generally seen in passing from one quite different soil to another: not only the proportional numbers of the heath-plants were wholly changed, but twelve species of plants (not counting grasses and carices) flourished in the plantations, which could not be found on the heath. The effect on the insects must have been still greater, for six insectivorous birds were very common in the plantations, which were not to be seen on the heath; and the heath was frequented by two or three distinct insectivorous birds. Here we see how potent has been the effect of the introduction of a single tree, nothing whatever else having been done, with the exception that the land had been enclosed, so that cattle could not enter. But how important an element enclosure is, I plainly saw near Farnham, in Surrey. Here there are extensive heaths, with a few clumps of old Scotch firs on the distant hill-tops: within the last ten years large spaces have been enclosed, and self-sown firs are now springing up in multitudes, so close together that all cannot live.

When I ascertained that these young trees had not been sown or planted, I was so much surprised at their numbers that I went to several points of view, whence I could examine hundreds of acres of the unenclosed heath, and literally I could not see a single Scotch fir, except the old planted clumps. But on looking closely between the stems of the heath, I found a multitude of seedlings and little trees, which had been perpetually browsed down by the cattle. In one square yard, at a point some hundreds yards distant from one of the old clumps, I counted thirty-two little trees; and one of them, judging from the rings of growth, had during twenty-six years tried to raise its head above the stems of the heath, and had failed. No wonder that, as soon as the land was enclosed, it became thickly clothed with vigorously growing young firs. Yet the heath was so extremely barren and so extensive that no one would ever have imagined that cattle would have so closely and effectually searched it for food.

Here we see that cattle absolutely determine the existence of the Scotch fir; but in several parts of the world insects determine the existence of cattle. Perhaps Paraguay offers the most curious instance of this; for here neither cattle nor horses nor dogs have ever run wild, though they swarm southward and northward in a feral state; and Azara and Rengger have shown that this is caused by the greater number in Paraguay of a certain fly, which lays its eggs in the navels of these animals when first born. The increase of these flies, numerous as they are, must be habitually checked by some means, probably by birds. Hence, if certain insectivorous birds (whose numbers are probably regulated by hawks or beasts of prey) were to increase in Paraguay, the flies would decrease–then cattle and horses would become feral, and this would certainly greatly alter (as indeed I have observed in parts of South America) the vegetation: this again would largely affect the insects; and this, as we just have seen in Staffordshire, the

insectivorous birds, and so onwards in ever-increasing circles of complexity. We began this series by insectivorous birds, and we have ended with them. Not that in nature the relations can ever be as simple as this. Battle within battle must ever be recurring with varying success; and yet in the long-run the forces are so nicely balanced, that the face of nature remains uniform for long periods of time, though assuredly the merest trifle would often give the victory to one organic being over another. Nevertheless so profound is our ignorance, and so high our presumption, that we marvel when we hear of the extinction of an organic being; and as we do not see the cause, we invoke cataclysms to desolate the world, or invent laws on the duration of the forms of life!

I am tempted to give one more instance showing how plants and animals, most remote in the scale of nature, are bound together by a web of complex relations. I shall hereafter have occasion to show that the exotic Lobelia fulgens, in this part of England, is never visited by insects, and consequently, from its peculiar structure, never can set a seed. Many of our orchidaceous plants absolutely require the visits of moths to remove their pollen-masses and thus to fertilise them. I have, also, reason to believe that humble-bees are indispensable to the fertilisation of the heartsease (Viola tricolor), for other bees do not visit this flower. From experiments which I have tried, I have found that the visits of bees, if not indispensable, are at least highly beneficial to the fertilisation of our clovers; but humble-bees alone visit the common red clover (Trifolium pratense), as other bees cannot reach the nectar. Hence I have very little doubt, that if the whole genus of humble-bees became extinct or very rare in England, the heartsease and red clover would become very rare, or wholly disappear. The number of humble-bees in any district depends in a great degree on the number of field-mice, which destroy their combs and nests; and Mr. H. Newman, who has long attended to the habits of humble-bees, believes that 'more than two thirds of them are thus destroyed all over England.' Now the number of mice is largely dependent, as every one knows, on the number of cats; and Mr. Newman says, 'Near villages and small towns I have found the nests of humble-bees more numerous than elsewhere, which I attribute to the number of cats that destroy the mice.' Hence it is quite credible that the presence of a feline animal in large numbers in a district might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in that district!

In the case of every species, many different checks, acting at different periods of life, and during different seasons or years, probably come into play; some one check or some few being generally the most potent, but all concurring in determining the average number or even the existence of the species. In some cases it can be shown that widely-different checks act on the same species in different districts. When we look at the plants and bushes clothing an entangled bank, we are tempted to attribute their proportional numbers and kinds to what we call chance. But how false a view is this! Every one has heard that when an American forest is cut down, a very different vegetation springs up; but it has been observed that the trees now growing on the ancient Indian mounds, in the Southern United States, display the same beautiful diversity and proportion of kinds as in the surrounding virgin forests. What a struggle between the several kinds of trees must here have gone on during long centuries, each annually scattering its seeds by the thousand; what war between insect and insect–between insects, snails, and other animals with birds and beasts of prey–all striving to increase, and all feeding on each other or on the trees or their seeds and seedlings, or on the other plants which first clothed the ground and thus checked the growth of the trees! Throw up a handful of feathers, and all must fall to the ground according to definite laws; but how simple is this problem compared to the action and reaction of the innumerable plants and animals which have determined, in the course of centuries, the proportional numbers and kinds of trees now growing on the old Indian ruins!

The dependency of one organic being on another, as of a parasite on its prey, lies generally between beings remote in the scale of nature. This is often the case with those which may

strictly be said to struggle with each other for existence, as in the case of locusts and grass-feeding quadrupeds. But the struggle almost invariably will be most severe between the individuals of the same species, for they frequent the same districts, require the same food, and are exposed to the same dangers. In the case of varieties of the same species, the struggle will generally be almost equally severe, and we sometimes see the contest soon decided: for instance, if several varieties of wheat be sown together, and the mixed seed be resown, some of the varieties which best suit the soil or climate, or are naturally the most fertile, will beat the others and so yield more seed, and will consequently in a few years quite supplant the other varieties. To keep up a mixed stock of even such extremely close varieties as the variously coloured sweet-peas, they must be each year harvested separately, and the seed then mixed in due proportion, otherwise the weaker kinds will steadily decrease in numbers and disappear. So again with the varieties of sheep: it has been asserted that certain mountain-varieties will starve out other mountain-varieties, so that they cannot be kept together. The same result has followed from keeping together different varieties of the medicinal leech. It may even be doubted whether the varieties of any one of our domestic plants or animals have so exactly the same strength, habits, and constitution, that the original proportions of a mixed stock could be kept up for half a dozen generations, if they were allowed to struggle together, like beings in a state of nature, and if the seed or young were not annually sorted.

As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera. We see this in the recent extension over parts of the United States of one species of swallow having caused the decrease of another species. The recent increase of the missel-thrush in parts of Scotland has caused the decrease of the song-thrush. How frequently we hear of one species of rat taking the place of another species under the most different climates! In Russia the small Asiatic cockroach has everywhere driven before it its great congener. One species of charlock will supplant another, and so in other cases. We can dimly see why the competition should be most severe between allied forms, which fill nearly the same place in the economy of nature; but probably in no one case could we precisely say why one species has been victorious over another in the great battle of life.

A corollary of the highest importance may be deduced from the foregoing remarks, namely, that the structure of every organic being is related, in the most essential yet often hidden manner, to that of all other organic beings, with which it comes into competition for food or residence, or from which it has to escape, or on which it preys. This is obvious in the structure of the teeth and talons of the tiger; and in that of the legs and claws of the parasite which clings to the hair on the tiger's body. But in the beautifully plumed seed of the dandelion, and in the flattened and fringed legs of the water-beetle, the relation seems at first confined to the elements of air and water. Yet the advantage of plumed seeds no doubt stands in the closest relation to the land being already thickly clothed by other plants; so that the seeds may be widely distributed and fall on unoccupied ground. In the water-beetle, the structure of its legs, so well adapted for diving, allows it to compete with other aquatic insects, to hunt for its own prey, and to escape serving as prey to other animals. The store of nutriment laid up within the seeds of many plants seems at first sight to have no sort of relation to other plants. But from the strong growth of young plants produced from such seeds (as peas and beans), when sown in the midst of long grass, I suspect that the chief use of the nutriment in the seed is to favour the growth of the young seedling, whilst struggling with other plants growing vigorously all around.

Look at a plant in the midst of its range, why does it not double or quadruple its numbers? We know that it can perfectly well withstand a little more heat or cold, dampness or dryness, for elsewhere it ranges into slightly hotter or colder, damper or drier districts. In this case we can clearly see that if we wished in imagination to give the plant the power of increasing in

number, we should have to give it some advantage over its competitors, or over the animals which preyed on it. On the confines of its geographical range, a change of constitution with respect to climate would clearly be an advantage to our plant; but we have reason to believe that only a few plants or animals range so far, that they are destroyed by the rigour of the climate alone. Not until we reach the extreme confines of life, in the arctic regions or on the borders of an utter desert, will competition cease. The land may be extremely cold or dry, yet there will be competition between some few species, or between the individuals of the same species, for the warmest or dampest spots.

Hence, also, we can see that when a plant or animal is placed in a new country amongst new competitors, though the climate may be exactly the same as in its former home, yet the conditions of its life will generally be changed in an essential manner. If we wished to increase its average numbers in its new home, we should have to modify it in a different way to what we should have done in its native country; for we should have to give it some advantage over a different set of competitors or enemies.

It is good thus to try in our imagination to give any form some advantage over another. Probably in no single instance should we know what to do, so as to succeed. It will convince us of our ignorance on the mutual relations of all organic beings; a conviction as necessary, as it seems to be difficult to acquire. All that we can do, is to keep steadily in mind that each organic being is striving to increase at a geometrical ratio; that each at some period of its life, during some season of the year, during each generation or at intervals, has to struggle for life, and to suffer great destruction. When we reflect on this struggle, we may console ourselves with the full belief, that the war of nature is not incessant, that no fear is felt, that death is generally prompt, and that the vigorous, the healthy, and the happy survive and multiply.

Chapter IV

Natural Selection

Natural Selection – its power compared with man's selection – its power on characters of trifling importance – its power at all ages and on both sexes – Sexual Selection – On the generality of intercrosses between individuals of the same species – Circumstances favourable and unfavourable to Natural Selection, namely, intercrossing, isolation, number of individuals – Slow action – Extinction caused by Natural Selection – Divergence of Character, related to the diversity of inhabitants of any small area, and to naturalisation – Action of Natural Selection, through Divergence of Character and Extinction, on the descendants from a common parent – Explains the Grouping of all organic beings.

How will the struggle for existence, discussed too briefly in the last chapter, act in regard to variation? Can the principle of selection, which we have seen is so potent in the hands of man, apply in nature? I think we shall see that it can act most effectually. Let it be borne in mind in what an endless number of strange peculiarities our domestic productions, and, in a lesser degree, those under nature, vary; and how strong the hereditary tendency is. Under domestication, it may be truly said that the whole organisation becomes in some degree plastic. Let it be borne in mind how infinitely complex and close-fitting are the mutual relations of all organic beings to each other and to their physical conditions of life. Can it, then, be thought improbable, seeing that variations useful to man have undoubtedly occurred, that other variations useful in some way to each being in the great and complex battle of life, should sometimes occur in the course of thousands of generations? If such do occur, can we doubt (remembering that many more individuals are born than can possibly survive) that individuals having any advantage, however slight, over others, would have the best chance of surviving and of procreating their kind? On the other hand, we may feel sure that any variation in the least degree injurious would be rigidly destroyed. This preservation of favourable variations and the rejection of injurious variations, I call Natural Selection. Variations neither useful nor injurious would not be affected by natural selection, and would be left a fluctuating element, as perhaps we see in the species called polymorphic.

We shall best understand the probable course of natural selection by taking the case of a country undergoing some physical change, for instance, of climate. The proportional numbers of its inhabitants would almost immediately undergo a change, and some species might become extinct. We may conclude, from what we have seen of the intimate and complex manner in which the inhabitants of each country are bound together, that any change in the numerical proportions of some of the inhabitants, independently of the change of climate itself, would most seriously affect many of the others. If the country were open on its borders, new forms would certainly immigrate, and this also would seriously disturb the relations of some of the former inhabitants. Let it be remembered how powerful the influence of a single introduced tree or mammal has been shown to be. But in the case of an island, or of a country partly surrounded by barriers, into which new and better adapted forms could not freely enter, we should then have places in the economy of nature which would assuredly be better filled up, if some of the original inhabitants were in some manner modified; for, had the area been open to immigration, these same places would have been seized on by intruders. In such case, every slight modification, which in the course of ages chanced to arise, and which in any way favoured the individuals of any of the species, by better adapting them to their altered conditions, would tend to be preserved; and natural selection would thus have free scope for the work of improvement.

We have reason to believe, as stated in the first chapter, that a change in the conditions of life, by specially acting on the reproductive system, causes or increases variability; and in the foregoing case the conditions of life are supposed to have undergone a change, and this would manifestly be favourable to natural selection, by giving a better chance of profitable variations occurring; and unless profitable variations do occur, natural selection can do nothing. Not that, as I believe, any extreme amount of variability is necessary; as man can certainly produce great results by adding up in any given direction mere individual differences, so could Nature, but far more easily, from having incomparably longer time at her disposal. Nor do I believe that any great physical change, as of climate, or any unusual degree of isolation to check immigration, is actually necessary to produce new and unoccupied places for natural selection to fill up by modifying and improving some of the varying inhabitants. For as all the inhabitants of each country are struggling together with nicely balanced forces, extremely slight modifications in the structure or habits of one inhabitant would often give it an advantage over others; and still further modifications of the same kind would often still further increase the advantage. No country can be named in which all the native inhabitants are now so perfectly adapted to each other and to the physical conditions under which they live, that none of them could anyhow be improved; for in all countries, the natives have been so far conquered by naturalised productions, that they have allowed foreigners to take firm possession of the land. And as foreigners have thus everywhere beaten some of the natives, we may safely conclude that the natives might have been modified with advantage, so as to have better resisted such intruders.

As man can produce and certainly has produced a great result by his methodical and unconscious means of selection, what may not nature effect? Man can act only on external and visible characters: nature cares nothing for appearances, except in so far as they may be useful to any being. She can act on every internal organ, on every shade of constitutional difference, on the whole machinery of life. Man selects only for his own good; Nature only for that of the being which she tends. Every selected character is fully exercised by her; and the being is placed under well-suited conditions of life. Man keeps the natives of many climates in the same country; he seldom exercises each selected character in some peculiar and fitting manner; he feeds a long and a short beaked pigeon on the same food; he does not exercise a long-backed or long-legged quadruped in any peculiar manner; he exposes sheep with long and short wool to the same climate. He does not allow the most vigorous males to struggle for the females. He does not rigidly destroy all inferior animals, but protects during each varying season, as far as lies in his power, all his productions. He often begins his selection by some half-monstrous form; or at least by some modification prominent enough to catch his eye, or to be plainly useful to him. Under nature, the slightest difference of structure or constitution may well turn the nicely-balanced scale in the struggle for life, and so be preserved. How fleeting are the wishes and efforts of man! How short his time! And consequently how poor will his products be, compared with those accumulated by nature during whole geological periods. Can we wonder, then, that nature's productions should be far 'truer' in character than man's productions; that they should be infinitely better adapted to the most complex conditions of life, and should plainly bear the stamp of far higher workmanship?

It may be said that natural selection is daily and hourly scrutinising, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life. We see nothing of these slow changes in progress, until the hand of time has marked the long lapse of ages, and then so imperfect is our view into long past geological ages, that we only see that the forms of life are now different from what they formerly were.

Although natural selection can act only through and for the good of each being, yet characters and structures, which we are apt to consider as of very trifling importance, may thus

be acted on. When we see leaf-eating insects green, and bark-feeders mottled-grey; the alpine ptarmigan white in winter, the red-grouse the colour of heather, and the black-grouse that of peaty earth, we must believe that these tints are of service to these birds and insects in preserving them from danger. Grouse, if not destroyed at some period of their lives, would increase in countless numbers; they are known to suffer largely from birds of prey; and hawks are guided by eyesight to their prey, –so much so, that on parts of the Continent persons are warned not to keep white pigeons, as being the most liable to destruction. Hence I can see no reason to doubt that natural selection might be most effective in giving the proper colour to each kind of grouse, and in keeping that colour, when once acquired, true and constant. Nor ought we to think that the occasional destruction of an animal of any particular colour would produce little effect: we should remember how essential it is in a flock of white sheep to destroy every lamb with the faintest trace of black. In plants the down on the fruit and the colour of the flesh are considered by botanists as characters of the most trifling importance: yet we hear from an excellent horticulturist, Downing, that in the United States smooth-skinned fruits suffer far more from a beetle, a curculio, than those with down; that purple plums suffer far more from a certain disease than yellow plums; whereas another disease attacks yellow-fleshed peaches far more than those with other coloured flesh. If, with all the aids of art, these slight differences make a great difference in cultivating the several varieties, assuredly, in a state of nature, where the trees would have to struggle with other trees and with a host of enemies, such differences would effectually settle which variety, whether a smooth or downy, a yellow or purple fleshed fruit, should succeed.

In looking at many small points of difference between species, which, as far as our ignorance permits us to judge, seem to be quite unimportant, we must not forget that climate, food, &c., probably produce some slight and direct effect. It is, however, far more necessary to bear in mind that there are many unknown laws of correlation of growth, which, when one part of the organisation is modified through variation, and the modifications are accumulated by natural selection for the good of the being, will cause other modifications, often of the most unexpected nature.

As we see that those variations which under domestication appear at any particular period of life, tend to reappear in the offspring at the same period; –for instance, in the seeds of the many varieties of our culinary and agricultural plants; in the caterpillar and cocoon stages of the varieties of the silkworm; in the eggs of poultry, and in the colour of the down of their chickens; in the horns of our sheep and cattle when nearly adult; –so in a state of nature, natural selection will be enabled to act on and modify organic beings at any age, by the accumulation of profitable variations at that age, and by their inheritance at a corresponding age. If it profit a plant to have its seeds more and more widely disseminated by the wind, I can see no greater difficulty in this being effected through natural selection, than in the cotton-planter increasing and improving by selection the down in the pods on his cotton-trees. Natural selection may modify and adapt the larva of an insect to a score of contingencies, wholly different from those, which concern the mature insect. These modifications will no doubt affect, through the laws of correlation, the structure of the adult; and probably in the case of those insects which live only for a few hours, and which never feed, a large part of their structure is merely the correlated result of successive changes in the structure of their larvae. So, conversely, modifications in the adult will probably often affect the structure of the larva; but in all cases natural selection will ensure that modifications consequent on other modifications at a different period of life, shall not be in the least degree injurious: for if they became so, they would cause the extinction of the species.

Natural selection will modify the structure of the young in relation to the parent, and of the parent in relation to the young. In social animals it will adapt the structure of each individual for the benefit of the community; if each in consequence profits by the selected change. What natural selection cannot do, is to modify the structure of one species, without giving it any

advantage, for the good of another species; and though statements to this effect may be found in works of natural history, I cannot find one case which will bear investigation. A structure used only once in an animal's whole life, if of high importance to it, might be modified to any extent by natural selection; for instance, the great jaws possessed by certain insects, and used exclusively for opening the cocoon–or the hard tip to the beak of nestling birds, used for breaking the egg. It has been asserted, that of the best short-beaked tumbler-pigeons more perish in the egg than are able to get out of it; so that fanciers assist in the act of hatching. Now, if nature had to make the beak of a full-grown pigeon very short for the bird's own advantage, the process of modification would be very slow, and there would be simultaneously the most rigorous selection of the young birds within the egg, which had the most powerful and hardest beaks, for all with weak beaks would inevitably perish: or, more delicate and more easily broken shells might be selected, the thickness of the shell being known to vary like every other structure.

Sexual Selection. – Inasmuch as peculiarities often appear under domestication in one sex and become hereditarily attached to that sex, the same fact probably occurs under nature, and if so, natural selection will be able to modify one sex in its functional relations to the other sex, or in relation to wholly different habits of life in the two sexes, as is sometimes the case with insects. And this leads me to say a few words on what I call Sexual Selection. This depends, not on a struggle for existence, but on a struggle between the males for possession of the females; the result is not death to the unsuccessful competitor, but few or no offspring. Sexual selection is, therefore, less rigorous than natural selection. Generally, the most vigorous males, those which are best fitted for their places in nature, will leave most progeny. But in many cases, victory will depend not on general vigour, but on having special weapons, confined to the male sex. A hornless stag or spurless cock would have a poor chance of leaving offspring. Sexual selection by always allowing the victor to breed might surely give indomitable courage, length to the spur, and strength to the wing to strike in the spurred leg, as well as the brutal cock-fighter, who knows well that he can improve his breed by careful selection of the best cocks. How low in the scale of nature this law of battle descends, I know not; male alligators have been described as fighting, bellowing, and whirling round, like Indians in a war-dance, for the possession of the females; male salmons have been seen fighting all day long; male stag-beetles often bear wounds from the huge mandibles of other males. The war is, perhaps, severest between the males of polygamous animals, and these seem oftenest provided with special weapons. The males of carnivorous animals are already well armed; though to them and to others, special means of defence may be given through means of sexual selection, as the mane to the lion, the shoulder-pad to the boar, and the hooked jaw to the male salmon; for the shield may be as important for victory, as the sword or spear.

Amongst birds, the contest is often of a more peaceful character. All those who have attended to the subject, believe that there is the severest rivalry between the males of many species to attract by singing the females. The rock-thrush of Guiana, birds of Paradise, and some others, congregate; and successive males display their gorgeous plumage and perform strange antics before the females, which standing by as spectators, at last choose the most attractive partner. Those who have closely attended to birds in confinement well know that they often take individual preferences and dislikes: thus Sir R. Heron has described how one pied peacock was eminently attractive to all his hen birds. It may appear childish to attribute any effect to such apparently weak means: I cannot here enter on the details necessary to support this view; but if man can in a short time give elegant carriage and beauty to his bantams, according to his standard of beauty, I can see no good reason to doubt that female birds, by selecting, during thousands of generations, the most melodious or beautiful males, according to their standard of beauty, might produce a marked effect. I strongly suspect that some well-known laws with respect to the plumage of male and female birds, in comparison

with the plumage of the young, can be explained on the view of plumage having been chiefly modified by sexual selection, acting when the birds have come to the breeding age or during the breeding season; the modifications thus produced being inherited at corresponding ages or seasons, either by the males alone, or by the males and females; but I have not space here to enter on this subject.

Thus it is, as I believe, that when the males and females of any animal have the same general habits of life, but differ in structure, colour, or ornament, such differences have been mainly caused by sexual selection; that is, individual males have had, in successive generations, some slight advantage over other males, in their weapons, means of defence, or charms; and have transmitted these advantages to their male offspring. Yet, I would not wish to attribute all such sexual differences to this agency: for we see peculiarities arising and becoming attached to the male sex in our domestic animals (as the wattle in male carriers, horn-like protuberances in the cocks of certain fowls, &c.), which we cannot believe to be either useful to the males in battle, or attractive to the females. We see analogous cases under nature, for instance, the tuft of hair on the breast of the turkey-cock, which can hardly be either useful or ornamental to this bird; –indeed, had the tuft appeared under domestication, it would have been called a monstrosity.

Illustrations of the action of Natural Selection. – In order to make it clear how, as I believe, natural selection acts, I must beg permission to give one or two imaginary illustrations. Let us take the case of a wolf, which preys on various animals, securing some by craft, some by strength, and some by fleetness; and let us suppose that the fleetest prey, a deer for instance, had from any change in the country increased in numbers, or that other prey had decreased in numbers, during that season of the year when the wolf is hardest pressed for food. I can under such circumstances see no reason to doubt that the swiftest and slimmest wolves would have the best chance of surviving, and so be preserved or selected, –provided always that they retained strength to master their prey at this or at some other period of the year, when they might be compelled to prey on other animals. I can see no more reason to doubt this, than that man can improve the fleetness of his greyhounds by careful and methodical selection, or by that unconscious selection which results from each man trying to keep the best dogs without any thought of modifying the breed.

Even without any change in the proportional numbers of the animals on which our wolf preyed, a cub might be born with an innate tendency to pursue certain kinds of prey. Nor can this be thought very improbable; for we often observe great differences in the natural tendencies of our domestic animals; one cat, for instance, taking to catch rats, another mice; one cat, according to Mr. St. John, bringing home winged game, another hares or rabbits, and another hunting on marshy ground and almost nightly catching woodcocks or snipes. The tendency to catch rats rather than mice is known to be inherited. Now, if any slight innate change of habit or of structure benefited an individual wolf, it would have the best chance of surviving and of leaving offspring. Some of its young would probably inherit the same habits or structure, and by the repetition of this process, a new variety might be formed which would either supplant or coexist with the parent-form of wolf. Or, again, the wolves inhabiting a mountainous district, and those frequenting the lowlands, would naturally be forced to hunt different prey; and from the continued preservation of the individuals best fitted for the two sites, two varieties might slowly be formed. These varieties would cross and blend where they met; but to this subject of intercrossing we shall soon have to return. I may add, that, according to Mr. Pierce, there are two varieties of the wolf inhabiting the Catskill Mountains in the United States, one with a light greyhound-like form, which pursues deer, and the other more bulky, with shorter legs, which more frequently attacks the shepherd's flocks.

Let us now take a more complex case. Certain plants excrete a sweet juice, apparently for the sake of eliminating something injurious from their sap: this is effected by glands at the base

of the stipules in some Leguminosae, and at the back of the leaf of the common laurel. This juice, though small in quantity, is greedily sought by insects. Let us now suppose a little sweet juice or nectar to be excreted by the inner bases of the petals of a flower. In this case insects in seeking the nectar would get dusted with pollen, and would certainly often transport the pollen from one flower to the stigma of another flower. The flowers of two distinct individuals of the same species would thus get crossed; and the act of crossing, we have good reason to believe (as will hereafter be more fully alluded to), would produce very vigorous seedlings, which consequently would have the best chance of flourishing and surviving. Some of these seedlings would probably inherit the nectar-excreting power. Those individual flowers which had the largest glands or nectaries, and which excreted most nectar, would be oftenest visited by insects, and would be oftenest crossed; and so in the long-run would gain the upper hand. Those flowers, also, which had their stamens and pistils placed, in relation to the size and habits of the particular insects which visited them, so as to favour in any degree the transportal of their pollen from flower to flower, would likewise be favoured or selected. We might have taken the case of insects visiting flowers for the sake of collecting pollen instead of nectar; and as pollen is formed for the sole object of fertilisation, its destruction appears a simple loss to the plant; yet if a little pollen were carried, at first occasionally and then habitually, by the pollen-devouring insects from flower to flower, and a cross thus effected, although nine-tenths of the pollen were destroyed, it might still be a great gain to the plant; and those individuals which produced more and more pollen, and had larger and larger anthers, would be selected.

When our plant, by this process of the continued preservation or natural selection of more and more attractive flowers, had been rendered highly attractive to insects, they would, unintentionally on their part, regularly carry pollen from flower to flower; and that they can most effectually do this, I could easily show by many striking instances. I will give only one–not as a very striking case, but as likewise illustrating one step in the separation of the sexes of plants, presently to be alluded to. Some holly-trees bear only male flowers, which have four stamens producing rather a small quantity of pollen, and a rudimentary pistil; other holly-trees bear only female flowers; these have a full-sized pistil, and four stamens with shrivelled anthers, in which not a grain of pollen can be detected. Having found a female tree exactly sixty yards from a male tree, I put the stigmas of twenty flowers, taken from different branches, under the microscope, and on all, without exception, there were pollen-grains, and on some a profusion of pollen. As the wind had set for several days from the female to the male tree, the pollen could not thus have been carried. The weather had been cold and boisterous, and therefore not favourable to bees, nevertheless every female flower which I examined had been effectually fertilised by the bees, accidentally dusted with pollen, having flown from tree to tree in search of nectar. But to return to our imaginary case: as soon as the plant had been rendered so highly attractive to insects that pollen was regularly carried from flower to flower, another process might commence. No naturalist doubts the advantage of what has been called the 'physiological division of labour;' hence we may believe that it would be advantageous to a plant to produce stamens alone in one flower or on one whole plant, and pistils alone in another flower or on another plant. In plants under culture and placed under new conditions of life, sometimes the male organs and sometimes the female organs become more or less impotent; now if we suppose this to occur in ever so slight a degree under nature, then as pollen is already carried regularly from flower to flower, and as a more complete separation of the sexes of our plant would be advantageous on the principle of the division of labour, individuals with this tendency more and more increased, would be continually favoured or selected, until at last a complete separation of the sexes would be effected.

Let us now turn to the nectar-feeding insects in our imaginary case: we may suppose the plant of which we have been slowly increasing the nectar by continued selection, to be a common plant; and that certain insects depended in main part on its nectar for food. I could give many facts, showing how anxious bees are to save time; for instance, their habit of cutting

holes and sucking the nectar at the bases of certain flowers, which they can, with a very little more trouble, enter by the mouth. Bearing such facts in mind, I can see no reason to doubt that an accidental deviation in the size and form of the body, or in the curvature and length of the proboscis, &c., far too slight to be appreciated by us, might profit a bee or other insect, so that an individual so characterised would be able to obtain its food more quickly, and so have a better chance of living and leaving descendants. Its descendants would probably inherit a tendency to a similar slight deviation of structure. The tubes of the corollas of the common red and incarnate clovers (Trifolium pratense and incarnatum) do not on a hasty glance appear to differ in length; yet the hive-bee can easily suck the nectar out of the incarnate clover, but not out of the common red clover, which is visited by humble-bees alone; so that whole fields of the red clover offer in vain an abundant supply of precious nectar to the hive-bee. Thus it might be a great advantage to the hive-bee to have a slightly longer or differently constructed proboscis. On the other hand, I have found by experiment that the fertility of clover greatly depends on bees visiting and moving parts of the corolla, so as to push the pollen on to the stigmatic surface. Hence, again, if humble-bees were to become rare in any country, it might be a great advantage to the red clover to have a shorter or more deeply divided tube to its corolla, so that the hive-bee could visit its flowers. Thus I can understand how a flower and a bee might slowly become, either simultaneously or one after the other, modified and adapted in the most perfect manner to each other, by the continued preservation of individuals presenting mutual and slightly favourable deviations of structure.

I am well aware that this doctrine of natural selection, exemplified in the above imaginary instances, is open to the same objections which were at first urged against Sir Charles Lyell's noble views on 'the modern changes of the earth, as illustrative of geology;' but we now very seldom hear the action, for instance, of the coast-waves, called a trifling and insignificant cause, when applied to the excavation of gigantic valleys or to the formation of the longest lines of inland cliffs. Natural selection can act only by the preservation and accumulation of infinitesimally small inherited modifications, each profitable to the preserved being; and as modern geology has almost banished such views as the excavation of a great valley by a single diluvial wave, so will natural selection, if it be a true principle, banish the belief of the continued creation of new organic beings, or of any great and sudden modification in their structure.

On the Intercrossing of Individuals. – I must here introduce a short digression. In the case of animals and plants with separated sexes, it is of course obvious that two individuals must always unite for each birth; but in the case of hermaphrodites this is far from obvious. Nevertheless I am strongly inclined to believe that with all hermaphrodites' two individuals, either occasionally or habitually, concur for the reproduction of their kind. This view, I may add, was first suggested by Andrew Knight. We shall presently see its importance; but I must here treat the subject with extreme brevity, though I have the materials prepared for an ample discussion. All vertebrate animals, all insects, and some other large groups of animals, pair for each birth. Modern research has much diminished the number of supposed hermaphrodites, and of real hermaphrodites a large number pair; that is, two individuals regularly unite for reproduction, which is all that concerns us. But still there are many hermaphrodite animals, which certainly do not habitually pair, and a vast majority of plants are hermaphrodites. What reason, it may be asked, is there for supposing in these cases that two individuals ever concur in reproduction? As it is impossible here to enter on details, I must trust to some general considerations alone.

In the first place, I have collected so large a body of facts, showing, in accordance with the almost universal belief of breeders, that with animals and plants a cross between different varieties, or between individuals of the same variety but of another strain, gives vigour and fertility to the offspring; and on the other hand, that close interbreeding diminishes vigour and

fertility; that these facts alone incline me to believe that it is a general law of nature (utterly ignorant though we be of the meaning of the law) that no organic being self-fertilises itself for an eternity of generations; but that a cross with another individual is occasionally–perhaps at very long intervals–indispensable.

On the belief that this is a law of nature, we can, I think, understand several large classes of facts, such as the following, which on any other view are inexplicable. Every hybridizer knows how unfavourable exposure to wet is to the fertilisation of a flower, yet what a multitude of flowers have their anthers and stigmas fully exposed to the weather! But if an occasional cross be indispensable, the fullest freedom for the entrance of pollen from another individual will explain this state of exposure, more especially as the plant's own anthers and pistil generally stand so close together that self-fertilisation seems almost inevitable. Many flowers, on the other hand, have their organs of fructification closely enclosed, as in the great papilionaceous or pea-family; but in several, perhaps in all, such flowers, there is a very curious adaptation between the structure of the flower and the manner in which bees suck the nectar; for, in doing this, they either push the flower's own pollen on the stigma, or bring pollen from another flower. So necessary are the visits of bees to papilionaceous flowers, that I have found, by experiments published elsewhere, that their fertility is greatly diminished if these visits be prevented. Now, it is scarcely possible that bees should fly from flower to flower, and not carry pollen from one to the other, to the great good, as I believe, of the plant. Bees will act like a camel-hair pencil, and it is quite sufficient just to touch the anthers of one flower and then the stigma of another with the same brush to ensure fertilisation; but it must not be supposed that bees would thus produce a multitude of hybrids between distinct species; for if you bring on the same brush a plant's own pollen and pollen from another species, the former will have such a prepotent effect, that it will invariably and completely destroy, as has been shown by Gartner, any influence from the foreign pollen.

When the stamens of a flower suddenly spring towards the pistil, or slowly move one after the other towards it, the contrivance seems adapted solely to ensure self-fertilisation; and no doubt it is useful for this end: but, the agency of insects is often required to cause the stamens to spring forward, as Kolreuter has shown to be the case with the barberry; and curiously in this very genus, which seems to have a special contrivance for self-fertilisation, it is well known that if very closely-allied forms or varieties are planted near each other, it is hardly possible to raise pure seedlings, so largely do they naturally cross. In many other cases, far from there being any aids for self-fertilisation, there are special contrivances, as I could show from the writings of C. C. Sprengel and from my own observations, which effectually prevent the stigma receiving pollen from its own flower: for instance, in Lobelia fulgens, there is a really beautiful and elaborate contrivance by which every one of the infinitely numerous pollen-granules are swept out of the conjoined anthers of each flower, before the stigma of that individual flower is ready to receive them; and as this flower is never visited, at least in my garden, by insects, it never sets a seed, though by placing pollen from one flower on the stigma of another, I raised plenty of seedlings; and whilst another species of Lobelia growing close by, which is visited by bees, seeds freely. In very many other cases, though there be no special mechanical contrivance to prevent the stigma of a flower receiving its own pollen, yet, as C. C. Sprengel has shown, and as I can confirm, either the anthers burst before the stigma is ready for fertilisation, or the stigma is ready before the pollen of that flower is ready, so that these plants have in fact separated sexes, and must habitually be crossed. How strange are these facts! How strange that the pollen and stigmatic surface of the same flower, though placed so close together, as if for the very purpose of self-fertilisation, should in so many cases be mutually useless to each other! How simply are these facts explained on the view of an occasional cross with a distinct individual being advantageous or indispensable!

If several varieties of the cabbage, radish, onion, and of some other plants, be allowed to seed near each other, a large majority, as I have found, of the seedlings thus raised will turn out

mongrels: for instance, I raised 233 seedling cabbages from some plants of different varieties growing near each other, and of these only 78 were true to their kind, and some even of these were not perfectly true. Yet the pistil of each cabbage-flower is surrounded not only by its own six stamens, but also by those of the many other flowers on the same plant. How, then, comes it that such a vast number of the seedlings are mongrelized? I suspect that it must arise from the pollen of a distinct variety having a prepotent effect over a flower's own pollen; and that this is part of the general law of good being derived from the intercrossing of distinct individuals of the same species. When distinct species are crossed the case is directly the reverse, for a plant's own pollen is always prepotent over foreign pollen; but to this subject we shall return in a future chapter.

In the case of a gigantic tree covered with innumerable flowers, it may be objected that pollen could seldom be carried from tree to tree, and at most only from flower to flower on the same tree, and that flowers on the same tree can be considered as distinct individuals only in a limited sense. I believe this objection to be valid, but that nature has largely provided against it by giving to trees a strong tendency to bear flowers with separated sexes. When the sexes are separated, although the male and female flowers may be produced on the same tree, we can see that pollen must be regularly carried from flower to flower; and this will give a better chance of pollen being occasionally carried from tree to tree. That trees belonging to all Orders have their sexes more often separated than other plants, I find to be the case in this country; and at my request Dr. Hooker tabulated the trees of New Zealand, and Dr. Asa Gray those of the United States, and the result was as I anticipated. On the other hand, Dr. Hooker has recently informed me that he finds that the rule does not hold in Australia; and I have made these few remarks on the sexes of trees simply to call attention to the subject.

Turning for a very brief space to animals: on the land there are some hermaphrodites, as land-mollusca and earth-worms; but these all pair. As yet I have not found a single case of a terrestrial animal which fertilises itself. We can understand this remarkable fact, which offers so strong a contrast with terrestrial plants, on the view of an occasional cross being indispensable, by considering the medium in which terrestrial animals live, and the nature of the fertilising element; for we know of no means, analogous to the action of insects and of the wind in the case of plants, by which an occasional cross could be effected with terrestrial animals without the concurrence of two individuals. Of aquatic animals, there are many self-fertilising hermaphrodites; but here currents in the water offer an obvious means for an occasional cross. And, as in the case of flowers, I have as yet failed, after consultation with one of the highest authorities, namely, Professor Huxley, to discover a single case of an hermaphrodite animal with the organs of reproduction so perfectly enclosed within the body, that access from without and the occasional influence of a distinct individual can be shown to be physically impossible. Cirripedes long appeared to me to present a case of very great difficulty under this point of view; but I have been enabled, by a fortunate chance, elsewhere to prove that two individuals, though both are self-fertilising hermaphrodites, do sometimes cross.

It must have struck most naturalists as a strange anomaly that, in the case of animals and plants, species of the same family and even of the same genus, though agreeing closely with each other in almost their whole organisation, yet are not rarely, some of them hermaphrodites, and some of them unisexual. But if, in fact, all hermaphrodites do occasionally intercross with other individuals, the difference between hermaphrodites and unisexual species, as far as function is concerned, becomes very small.

From these several considerations and from the many special facts which I have collected, but which I am not here able to give, I am strongly inclined to suspect that, both in the vegetable and animal kingdoms, an occasional intercross with a distinct individual is a law of nature. I am well aware that there are, on this view, many cases of difficulty, some of which I

am trying to investigate. Finally then, we may conclude that in many organic beings, a cross between two individuals is an obvious necessity for each birth; in many others it occurs perhaps only at long intervals; but in none, as I suspect, can self-fertilisation go on for perpetuity.

Circumstances favourable to Natural Selection. – This is an extremely intricate subject. A large amount of inheritable and diversified variability is favourable, but I believe mere individual differences suffice for the work. A large number of individuals, by giving a better chance for the appearance within any given period of profitable variations, will compensate for a lesser amount of variability in each individual, and is, I believe, an extremely important element of success. Though nature grants vast periods of time for the work of natural selection, she does not grant an indefinite period; for as all organic beings are striving, it may be said, to seize on each place in the economy of nature, if any one species does not become modified and improved in a corresponding degree with its competitors, it will soon be exterminated.

In man's methodical selection, a breeder selects for some definite object, and free intercrossing will wholly stop his work. But when many men, without intending to alter the breed, have a nearly common standard of perfection, and all try to get and breed from the best animals, much improvement and modification surely but slowly follow from this unconscious process of selection, notwithstanding a large amount of crossing with inferior animals. Thus it will be in nature; for within a confined area, with some place in its polity not so perfectly occupied as might be, natural selection will always tend to preserve all the individuals varying in the right direction, though in different degrees, so as better to fill up the unoccupied place. But if the area be large, its several districts will almost certainly present different conditions of life; and then if natural selection be modifying and improving a species in the several districts, there will be intercrossing with the other individuals of the same species on the confines of each. And in this case the effects of intercrossing can hardly be counterbalanced by natural selection always tending to modify all the individuals in each district in exactly the same manner to the conditions of each; for in a continuous area, the conditions will generally graduate away insensibly from one district to another. The intercrossing will most affect those animals which unite for each birth, which wander much, and which do not breed at a very quick rate. Hence in animals of this nature, for instance in birds, varieties will generally be confined to separated countries; and this I believe to be the case. In hermaphrodite organisms which cross only occasionally, and likewise in animals which unite for each birth, but which wander little and which can increase at a very rapid rate, a new and improved variety might be quickly formed on any one spot, and might there maintain itself in a body, so that whatever intercrossing took place would be chiefly between the individuals of the same new variety. A local variety when once thus formed might subsequently slowly spread to other districts. On the above principle, nurserymen always prefer getting seed from a large body of plants of the same variety, as the chance of intercrossing with other varieties is thus lessened.

Even in the case of slow-breeding animals, which unite for each birth, we must not overrate the effects of intercrosses in retarding natural selection; for I can bring a considerable catalogue of facts, showing that within the same area, varieties of the same animal can long remain distinct, from haunting different stations, from breeding at slightly different seasons, or from varieties of the same kind preferring to pair together.

Intercrossing plays a very important part in nature in keeping the individuals of the same species, or of the same variety, true and uniform in character. It will obviously thus act far more efficiently with those animals which unite for each birth; but I have already attempted to show that we have reason to believe that occasional intercrosses take place with all animals and with all plants. Even if these take place only at long intervals, I am convinced that the young thus produced will gain so much in vigour and fertility over the offspring from

long-continued self-fertilisation, that they will have a better chance of surviving and propagating their kind; and thus, in the long run, the influence of intercrosses, even at rare intervals, will be great. If there exist organic beings which never intercross, uniformity of character can be retained amongst them, as long as their conditions of life remain the same, only through the principle of inheritance, and through natural selection destroying any which depart from the proper type; but if their conditions of life change and they undergo modification, uniformity of character can be given to their modified offspring, solely by natural selection preserving the same favourable variations.

Isolation, also, is an important element in the process of natural selection. In a confined or isolated area, if not very large, the organic and inorganic conditions of life will generally be in a great degree uniform; so that natural selection will tend to modify all the individuals of a varying species throughout the area in the same manner in relation to the same conditions. Intercrosses, also, with the individuals of the same species, which otherwise would have inhabited the surrounding and differently circumstanced districts, will be prevented. But isolation probably acts more efficiently in checking the immigration of better adapted organisms, after any physical change, such as of climate or elevation of the land, &c.; and thus new places in the natural economy of the country are left open for the old inhabitants to struggle for, and become adapted to, through modifications in their structure and constitution. Lastly, isolation, by checking immigration and consequently competition, will give time for any new variety to be slowly improved; and this may sometimes be of importance in the production of new species. If, however, an isolated area be very small, either from being surrounded by barriers, or from having very peculiar physical conditions, the total number of the individuals supported on it will necessarily be very small; and fewness of individuals will greatly retard the production of new species through natural selection, by decreasing the chance of the appearance of favourable variations.

If we turn to nature to test the truth of these remarks, and look at any small isolated area, such as an oceanic island, although the total number of the species inhabiting it, will be found to be small, as we shall see in our chapter on geographical distribution; yet of these species a very large proportion are endemic, –that is, have been produced there, and nowhere else. Hence an oceanic island at first sight seems to have been highly favourable for the production of new species. But we may thus greatly deceive ourselves, for to ascertain whether a small isolated area, or a large open area like a continent, has been most favourable for the production of new organic forms, we ought to make the comparison within equal times; and this we are incapable of doing.

Although I do not doubt that isolation is of considerable importance in the production of new species, on the whole I am inclined to believe that largeness of area is of more importance, more especially in the production of species, which will prove capable of enduring for a long period, and of spreading widely. Throughout a great and open area, not only will there be a better chance of favourable variations arising from the large number of individuals of the same species there supported, but the conditions of life are infinitely complex from the large number of already existing species; and if some of these many species become modified and improved, others will have to be improved in a corresponding degree or they will be exterminated. Each new form, also, as soon as it has been much improved, will be able to spread over the open and continuous area, and will thus come into competition with many others. Hence more new places will be formed, and the competition to fill them will be more severe, on a large than on a small and isolated area. Moreover, great areas, though now continuous, owing to oscillations of level, will often have recently existed in a broken condition, so that the good effects of isolation will generally, to a certain extent, have concurred. Finally, I conclude that, although small isolated areas probably have been in some respects highly favourable for the production of new species, yet that the course of modification will generally have been more rapid on large areas; and what is more important,

that the new forms produced on large areas, which already have been victorious over many competitors, will be those that will spread most widely, will give rise to most new varieties and species, and will thus play an important part in the changing history of the organic world.

We can, perhaps, on these views, understand some facts which will be again alluded to in our chapter on geographical distribution; for instance, that the productions of the smaller continent of Australia have formerly yielded, and apparently are now yielding, before those of the larger Europaeo-Asiatic area. Thus, also, it is that continental productions have everywhere become so largely naturalised on islands. On a small island, the race for life will have been less severe, and there will have been less modification and less extermination. Hence, perhaps, it comes that the flora of Madeira, according to Oswald Heer, resembles the extinct tertiary flora of Europe. All fresh-water basins, taken together, make a small area compared with that of the sea or of the land; and, consequently, the competition between fresh-water productions will have been less severe than elsewhere; new forms will have been more slowly formed, and old forms more slowly exterminated. And it is in fresh water that we find seven genera of Ganoid fishes, remnants of a once preponderant order: and in fresh water we find some of the most anomalous forms now known in the world, as the Ornithorhynchus and Lepidosiren, which, like fossils, connect to a certain extent orders now widely separated in the natural scale. These anomalous forms may almost be called living fossils; they have endured to the present day, from having inhabited a confined area, and from having thus been exposed to less severe competition.

To sum up the circumstances favourable and unfavourable to natural selection, as far as the extreme intricacy of the subject permits. I conclude, looking to the future, that for terrestrial productions a large continental area, which will probably undergo many oscillations of level, and which consequently will exist for long periods in a broken condition, will be the most favourable for the production of many new forms of life, likely to endure long and to spread widely. For the area will first have existed as a continent, and the inhabitants, at this period numerous in individuals and kinds, will have been subjected to very severe competition. When converted by subsidence into large separate islands, there will still exist many individuals of the same species on each island: intercrossing on the confines of the range of each species will thus be checked: after physical changes of any kind, immigration will be prevented, so that new places in the polity of each island will have to be filled up by modifications of the old inhabitants; and time will be allowed for the varieties in each to become well modified and perfected. When, by renewed elevation, the islands shall be re-converted into a continental area, there will again be severe competition: the most favoured or improved varieties will be enabled to spread: there will be much extinction of the less improved forms, and the relative proportional numbers of the various inhabitants of the renewed continent will again be changed; and again there will be a fair field for natural selection to improve still further the inhabitants, and thus produce new species.

That natural selection will always act with extreme slowness, I fully admit. Its action depends on there being places in the polity of nature, which can be better occupied by some of the inhabitants of the country undergoing modification of some kind. The existence of such places will often depend on physical changes, which are generally very slow, and on the immigration of better-adapted forms having been checked. But the action of natural selection will probably still oftener depend on some of the inhabitants becoming slowly modified; the mutual relations of many of the other inhabitants being thus disturbed. Nothing can be effected, unless favourable variations occur, and variation itself is apparently always a very slow process. The process will often be greatly retarded by free intercrossing. Many will exclaim that these several causes are amply sufficient wholly to stop the action of natural selection. I do not believe so. On the other hand, I do believe that natural selection will always act very slowly, often only at long intervals of time, and generally on only a very few of the inhabitants of the same region at the same time. I further believe, that this very slow,

intermittent action of natural selection accords perfectly well with what geology tells us of the rate and manner at which the inhabitants of this world have changed.

Slow though the process of selection may be, if feeble man can do much by his powers of artificial selection, I can see no limit to the amount of change, to the beauty and infinite complexity of the coadaptations between all organic beings, one with another and with their physical conditions of life, which may be effected in the long course of time by nature's power of selection.

Extinction. – This subject will be more fully discussed in our chapter on Geology; but it must be here alluded to from being intimately connected with natural selection. Natural selection acts solely through the preservation of variations in some way advantageous, which consequently endure. But as from the high geometrical powers of increase of all organic beings, each area is already fully stocked with inhabitants, it follows that as each selected and favoured form increases in number, so will the less favoured forms decrease and become rare. Rarity, as geology tells us, is the precursor to extinction. We can, also, see that any form represented by few individuals will, during fluctuations in the seasons or in the number of its enemies, run a good chance of utter extinction. But we may go further than this; for as new forms are continually and slowly being produced, unless we believe that the number of specific forms goes on perpetually and almost indefinitely increasing, numbers inevitably must become extinct. That the number of specific forms has not indefinitely increased, geology shows us plainly; and indeed we can see reason why they should not have thus increased, for the number of places in the polity of nature is not indefinitely great, –not that we have any means of knowing that any one region has as yet got its maximum of species. Probably no region is as yet fully stocked, for at the Cape of Good Hope, where more species of plants are crowded together than in any other quarter of the world, some foreign plants have become naturalised, without causing, as far as we know, the extinction of any natives.

Furthermore, the species which are most numerous in individuals will have the best chance of producing within any given period favourable variations. We have evidence of this, in the facts given in the second chapter, showing that it is the common species, which afford the greatest number of recorded varieties, or incipient species. Hence, rare species will be less quickly modified or improved within any given period, and they will consequently be beaten in the race for life by the modified descendants of the commoner species.

From these several considerations I think it inevitably follows, that as new species in the course of time are formed through natural selection, others will become rarer and rarer, and finally extinct. The forms which stand in closest competition with those undergoing modification and improvement, will naturally suffer most. And we have seen in the chapter on the Struggle for Existence that it is the most closely-allied forms, –varieties of the same species, and species of the same genus or of related genera, –which, from having nearly the same structure, constitution, and habits, generally come into the severest competition with each other. Consequently, each new variety or species, during the progress of its formation, will generally press hardest on its nearest kindred, and tend to exterminate them. We see the same process of extermination amongst our domesticated productions, through the selection of improved forms by man. Many curious instances could be given showing how quickly new breeds of cattle, sheep, and other animals, and varieties of flowers, take the place of older and inferior kinds. In Yorkshire, it is historically known that the ancient black cattle were displaced by the long-horns, and that these 'were swept away by the short-horns' (I quote the words of an agricultural writer) 'as if by some murderous pestilence.'

Divergence of Character. – The principle, which I have designated by this term, is of high importance on my theory, and explains, as I believe, several important facts. In the first place, varieties, even strongly-marked ones, though having somewhat of the character of species–as

is shown by the hopeless doubts in many cases how to rank them–yet certainly differ from each other far less than do good and distinct species. Nevertheless, according to my view, varieties are species in the process of formation, or are, as I have called them, incipient species. How, then, does the lesser difference between varieties become augmented into the greater difference between species? That this does habitually happen, we must infer from most of the innumerable species throughout nature presenting well-marked differences; whereas varieties, the supposed prototypes and parents of future well-marked species, present slight and ill-defined differences. Mere chance, as we may call it, might cause one variety to differ in some character from its parents, and the offspring of this variety again to differ from its parent in the very same character and in a greater degree; but this alone would never account for so habitual and large an amount of difference as that between varieties of the same species and species of the same genus.

As has always been my practice, let us seek light on this head from our domestic productions. We shall here find something analogous. A fancier is struck by a pigeon having a slightly shorter beak; another fancier is struck by a pigeon having a rather longer beak; and on the acknowledged principle that 'fanciers do not and will not admire a medium standard, but like extremes,' they both go on (as has actually occurred with tumbler-pigeons) choosing and breeding from birds with longer and longer beaks, or with shorter and shorter beaks. Again, we may suppose that at an early period one man preferred swifter horses; another stronger and more bulky horses. The early differences would be very slight; in the course of time, from the continued selection of swifter horses by some breeders, and of stronger ones by others, the differences would become greater, and would be noted as forming two sub-breeds; finally, after the lapse of centuries, the sub-breeds would become converted into two well-established and distinct breeds. As the differences slowly become greater, the inferior animals with intermediate characters, being neither very swift nor very strong, will have been neglected, and will have tended to disappear. Here, then, we see in man's productions the action of what may be called the principle of divergence, causing differences, at first barely appreciable, steadily to increase, and the breeds to diverge in character both from each other and from their common parent.

But how, it may be asked, can any analogous principle apply in nature? I believe it can and does apply most efficiently, from the simple circumstance that the more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers.

We can clearly see this in the case of animals with simple habits. Take the case of a carnivorous quadruped, of which the number that can be supported in any country has long ago arrived at its full average. If its natural powers of increase be allowed to act, it can succeed in increasing (the country not undergoing any change in its conditions) only by its varying descendants seizing on places at present occupied by other animals: some of them, for instance, being enabled to feed on new kinds of prey, either dead or alive; some inhabiting new stations, climbing trees, frequenting water, and some perhaps becoming less carnivorous. The more diversified in habits and structure the descendants of our carnivorous animal became, the more places they would be enabled to occupy. What applies to one animal will apply throughout all time to all animals–that is, if they vary–for otherwise natural selection can do nothing. So it will be with plants. It has been experimentally proved, that if a plot of ground be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can thus be raised. The same has been found to hold good when first one variety and then several mixed varieties of wheat have been sown on equal spaces of ground. Hence, if any one species of grass were to go on varying, and those varieties were continually selected which differed from each other in at all the same manner as distinct species and genera of grasses differ from each other, a greater number of individual plants of this species

of grass, including its modified descendants, would succeed in living on the same piece of ground. And we well know that each species and each variety of grass is annually sowing almost countless seeds; and thus, as it may be said, is striving its utmost to increase its numbers. Consequently, I cannot doubt that in the course of many thousands of generations, the most distinct varieties of any one species of grass would always have the best chance of succeeding and of increasing in numbers, and thus of supplanting the less distinct varieties; and varieties, when rendered very distinct from each other, take the rank of species.

The truth of the principle, that the greatest amount of life can be supported by great diversification of structure, is seen under many natural circumstances. In an extremely small area, especially if freely open to immigration, and where the contest between individual and individual must be severe, we always find great diversity in its inhabitants. For instance, I found that a piece of turf, three feet by four in size, which had been exposed for many years to exactly the same conditions, supported twenty species of plants, and these belonged to eighteen genera and to eight orders, which shows how much these plants differed from each other. So it is with the plants and insects on small and uniform islets; and so in small ponds of fresh water. Farmers find that they can raise most food by a rotation of plants belonging to the most different orders: nature follows what may be called a simultaneous rotation. Most of the animals and plants which live close round any small piece of ground, could live on it (supposing it not to be in any way peculiar in its nature), and may be said to be striving to the utmost to live there; but, it is seen, that where they come into the closest competition with each other, the advantages of diversification of structure, with the accompanying differences of habit and constitution, determine that the inhabitants, which thus jostle each other most closely, shall, as a general rule, belong to what we call different genera and orders.

The same principle is seen in the naturalisation of plants through man's agency in foreign lands. It might have been expected that the plants which have succeeded in becoming naturalised in any land would generally have been closely allied to the indigenes; for these are commonly looked at as specially created and adapted for their own country. It might, also, perhaps have been expected that naturalised plants would have belonged to a few groups more especially adapted to certain stations in their new homes. But the case is very different; and Alph. De Candolle has well remarked in his great and admirable work, that floras gain by naturalisation, proportionally with the number of the native genera and species, far more in new genera than in new species. To give a single instance: in the last edition of Dr. Asa Gray's 'Manual of the Flora of the Northern United States,' 260 naturalised plants are enumerated, and these belong to 162 genera. We thus see that these naturalised plants are of a highly diversified nature. They differ, moreover, to a large extent from the indigenes, for out of the 162 genera, no less than 100 genera are not there indigenous, and thus a large proportional addition is made to the genera of these States.

By considering the nature of the plants or animals which have struggled successfully with the indigenes of any country, and have there become naturalised, we can gain some crude idea in what manner some of the natives would have had to be modified, in order to have gained an advantage over the other natives; and we may, I think, at least safely infer that diversification of structure, amounting to new generic differences, would have been profitable to them.

The advantage of diversification in the inhabitants of the same region is, in fact, the same as that of the physiological division of labour in the organs of the same individual body–a subject so well elucidated by Milne Edwards. No physiologist doubts that a stomach by being adapted to digest vegetable matter alone, or flesh alone, draws most nutriment from these substances. So in the general economy of any land, the more widely and perfectly the animals and plants are diversified for different habits of life, so will a greater number of individuals be capable of there supporting themselves. A set of animals, with their organisation but little diversified, could hardly compete with a set more perfectly diversified in structure. It may be doubted, for instance, whether the Australian marsupials, which are divided into groups

differing but little from each other, and feebly representing, as Mr. Waterhouse and others have remarked, our carnivorous, ruminant, and rodent mammals, could successfully compete with these well-pronounced orders. In the Australian mammals, we see the process of diversification in an early and incomplete stage of development.

After the foregoing discussion, which ought to have been much amplified, we may, I think, assume that the modified descendants of any one species will succeed by so much the better as they become more diversified in structure, and are thus enabled to encroach on places occupied by other beings. Now let us see how this principle of great benefit being derived from divergence of character, combined with the principles of natural selection and of extinction, will tend to act.

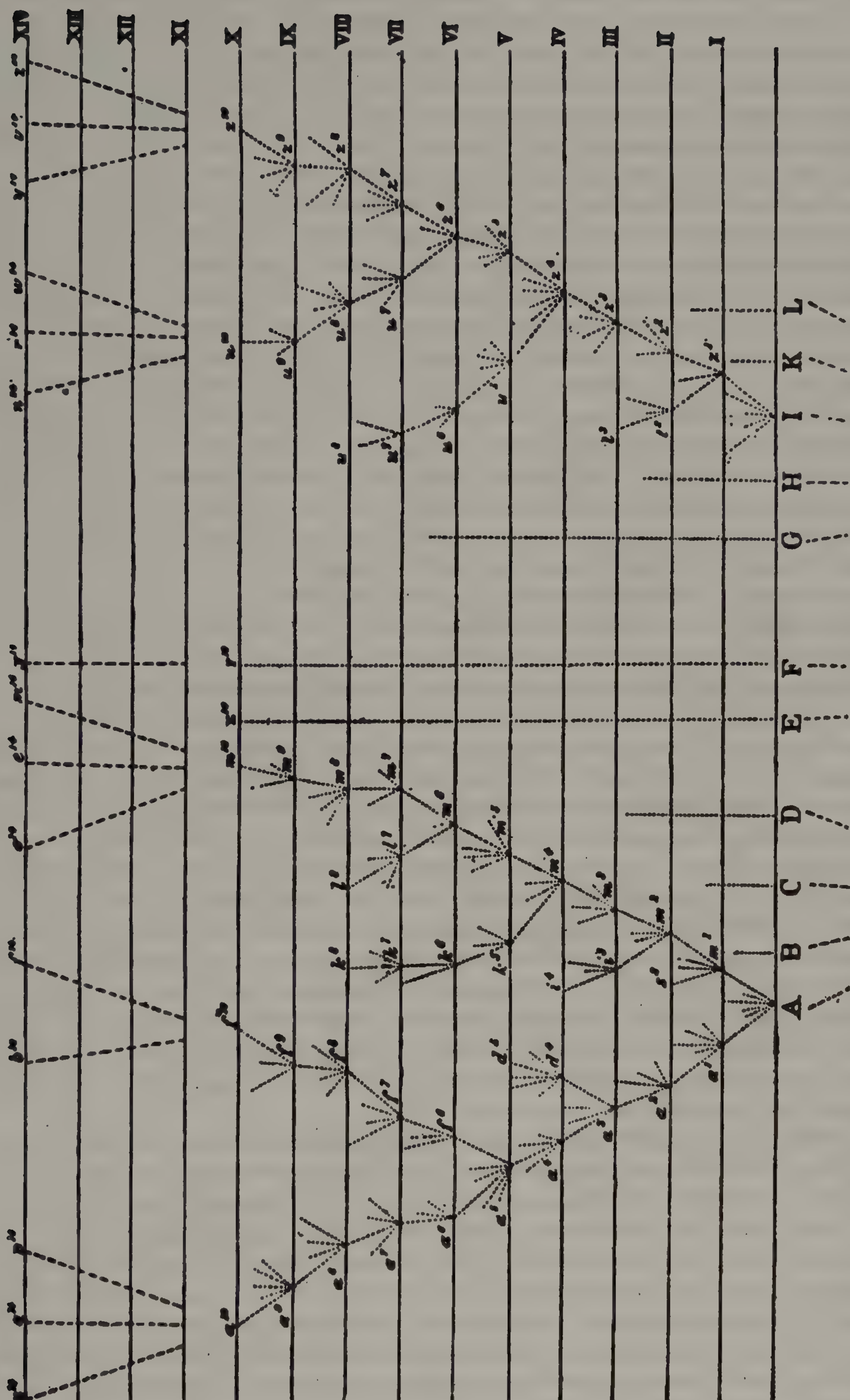
The accompanying diagram will aid us in understanding this rather perplexing subject. Let A to L represent the species of a genus large in its own country; these species are supposed to resemble each other in unequal degrees, as is so generally the case in nature, and as is represented in the diagram by the letters standing at unequal distances. I have said a large genus, because we have seen in the second chapter, that on an average more of the species of large genera vary than of small genera; and the varying species of the large genera present a greater number of varieties. We have, also, seen that the species, which are the commonest and the most widely-diffused, vary more than rare species with restricted ranges. Let (A) be a common, widely-diffused, and varying species, belonging to a genus large in its own country. The little fan of diverging dotted lines of unequal lengths proceeding from (A), may represent its varying offspring. The variations are supposed to be extremely slight, but of the most diversified nature; they are not supposed all to appear simultaneously, but often after long intervals of time; nor are they all supposed to endure for equal periods. Only those variations which are in some way profitable will be preserved or naturally selected. And here the importance of the principle of benefit being derived from divergence of character comes in; for this will generally lead to the most different or divergent variations (represented by the outer dotted lines) being preserved and accumulated by natural selection. When a dotted line reaches one of the horizontal lines, and is there marked by a small numbered letter, a sufficient amount of variation is supposed to have been accumulated to have formed a fairly well-marked variety, such as would be thought worthy of record in a systematic work.

The intervals between the horizontal lines in the diagram, may represent each a thousand generations; but it would have been better if each had represented ten thousand generations. After a thousand generations, species (A) is supposed to have produced two fairly well-marked varieties, namely a1 and m1. These two varieties will generally continue to be exposed to the same conditions which made their parents variable, and the tendency to variability is in itself hereditary, consequently they will tend to vary, and generally to vary in nearly the same manner as their parents varied. Moreover, these two varieties, being only slightly modified forms, will tend to inherit those advantages which made their common parent (A) more numerous than most of the other inhabitants of the same country; they will likewise partake of those more general advantages which made the genus to which the parent-species belonged, a large genus in its own country. And these circumstances we know to be favourable to the production of new varieties.

If, then, these two varieties be variable, the most divergent of their variations will generally be preserved during the next thousand generations. And after this interval, variety a1 is supposed in the diagram to have produced variety a2, which will, owing to the principle of divergence, differ more from (A) than did variety a1. Variety m1 is supposed to have produced two varieties, namely m2 and s2, differing from each other, and more considerably from their common parent (A). We may continue the process by similar steps for any length of time; some of the varieties, after each thousand generations, producing only a single variety, but in a more and more modified condition, some producing two or three varieties, and some failing to produce any. Thus the varieties or modified descendants, proceeding from the

common parent (A), will generally go on increasing in number and diverging in character. In the diagram the process is represented up to the ten-thousandth generation, and under a condensed and simplified form up to the fourteen-thousandth generation.

But I must here remark that I do not suppose that the process ever goes on so regularly as is represented in the diagram, though in itself made somewhat irregular. I am far from thinking that the most divergent varieties will invariably prevail and multiply: a medium form may often long endure, and may or may not produce more than one modified descendant; for natural selection will always act according to the nature of the places which are either unoccupied or not perfectly occupied by other beings; and this will depend on infinitely complex relations. But as a general rule, the more diversified in structure the descendants from any one species can be rendered, the more places they will be enabled to seize on, and the more their modified progeny will be increased. In our diagram the line of succession is broken at regular intervals by small numbered letters marking the successive forms which have become sufficiently distinct to be recorded as varieties. But these breaks are imaginary, and might have been inserted anywhere, after intervals long enough to have allowed the accumulation of a considerable amount of divergent variation.


A B C D E F G H I K L
I
II
III
IV
V
VI
VII
VIII
IX
X
XI
XII
XIII
XIV

As all the modified descendants from a common and widely-diffused species, belonging to a large genus, will tend to partake of the same advantages which made their parent successful in life, they will generally go on multiplying in number as well as diverging in character: this is represented in the diagram by the several divergent branches proceeding from (A). The modified offspring from the later and more highly improved branches in the lines of descent, will, it is probable, often take the place of, and so destroy, the earlier and less improved branches: this is represented in the diagram by some of the lower branches not reaching to the upper horizontal lines. In some cases I do not doubt that the process of modification will be confined to a single line of descent, and the number of the descendants will not be increased; although the amount of divergent modification may have been increased in the successive generations. This case would be represented in the diagram, if all the lines proceeding from (A) were removed, excepting that from a1 to a10. In the same way, for instance, the English race-horse and English pointer have apparently both gone on slowly diverging in character from their original stocks, without either having given off any fresh branches or races.

After ten thousand generations, species (A) is supposed to have produced three forms, a10, f10, and m10, which, from having diverged in character during the successive generations, will have come to differ largely, but perhaps unequally, from each other and from their common parent. If we suppose the amount of change between each horizontal line in our diagram to be excessively small, these three forms may still be only well-marked varieties; or they may have arrived at the doubtful category of sub-species; but we have only to suppose the steps in the process of modification to be more numerous or greater in amount, to convert these three forms into well-defined species: thus the diagram illustrates the steps by which the small differences distinguishing varieties are increased into the larger differences distinguishing species. By continuing the same process for a greater number of generations (as shown in the diagram in a condensed and simplified manner), we get eight species, marked by the letters between a14 and m14, all descended from (A). Thus, as I believe, species are multiplied and genera are formed.

In a large genus it is probable that more than one species would vary. In the diagram I have assumed that a second species (I) has produced, by analogous steps, after ten thousand generations, either two well-marked varieties (w10 and z10) or two species, according to the amount of change supposed to be represented between the horizontal lines. After fourteen thousand generations, six new species, marked by the letters n14 to z14, are supposed to have been produced. In each genus, the species, which are already extremely different in character, will generally tend to produce the greatest number of modified descendants; for these will have the best chance of filling new and widely different places in the polity of nature: hence in the diagram I have chosen the extreme species (A), and the nearly extreme species (I), as those which have largely varied, and have given rise to new varieties and species. The other nine species (marked by capital letters) of our original genus, may for a long period continue transmitting unaltered descendants; and this is shown in the diagram by the dotted lines not prolonged far upwards from want of space.

But during the process of modification, represented in the diagram, another of our principles, namely that of extinction, will have played an important part. As in each fully stocked country natural selection necessarily acts by the selected form having some advantage in the struggle for life over other forms, there will be a constant tendency in the improved descendants of any one species to supplant and exterminate in each stage of descent their predecessors and their original parent. For it should be remembered that the competition will generally be most severe between those forms which are most nearly related to each other in habits, constitution, and structure. Hence all the intermediate forms between the earlier and later states, that is between the less and more improved state of a species, as well as the original parent-species itself, will generally tend to become extinct. So it probably will be with many whole collateral lines of descent, which will be conquered by later and improved lines of descent. If, however, the modified offspring of a species get into some distinct country, or

become quickly adapted to some quite new station, in which child and parent do not come into competition, both may continue to exist.

If then our diagram be assumed to represent a considerable amount of modification, species (A) and all the earlier varieties will have become extinct, having been replaced by eight new species (a14 to m14); and (I) will have been replaced by six (n14 to z14) new species.

But we may go further than this. The original species of our genus were supposed to resemble each other in unequal degrees, as is so generally the case in nature; species (A) being more nearly related to B, C, and D, than to the other species; and species (I) more to G, H, K, L, than to the others. These two species (A) and (I), were also supposed to be very common and widely diffused species, so that they must originally have had some advantage over most of the other species of the genus. Their modified descendants, fourteen in number at the fourteen-thousandth generation, will probably have inherited some of the same advantages: they have also been modified and improved in a diversified manner at each stage of descent, so as to have become adapted to many related places in the natural economy of their country. It seems, therefore, to me extremely probable that they will have taken the places of, and thus exterminated, not only their parents (A) and (I), but likewise some of the original species which were most nearly related to their parents. Hence very few of the original species will have transmitted offspring to the fourteen-thousandth generation. We may suppose that only one (F), of the two species which were least closely related to the other nine original species, has transmitted descendants to this late stage of descent.

The new species in our diagram descended from the original eleven species, will now be fifteen in number. Owing to the divergent tendency of natural selection, the extreme amount of difference in character between species a14 and z14 will be much greater than that between the most different of the original eleven species. The new species, moreover, will be allied to each other in a widely different manner. Of the eight descendants from (A) the three marked a14, q14, p14, will be nearly related from having recently branched off from a10; b14 and f14, from having diverged at an earlier period from a5, will be in some degree distinct from the three first-named species; and lastly, o14, e14, and m14, will be nearly related one to the other, but from having diverged at the first commencement of the process of modification, will be widely different from the other five species, and may constitute a sub-genus or even a distinct genus.

The six descendants from (I) will form two sub-genera or even genera. But as the original species (I) differed largely from (A), standing nearly at the extreme points of the original genus, the six descendants from (I) will, owing to inheritance, differ considerably from the eight descendants from (A); the two groups, moreover, are supposed to have gone on diverging in different directions. The intermediate species, also (and this is a very important consideration), which connected the original species (A) and (I), have all become, excepting (F), extinct, and have left no descendants. Hence the six new species descended from (I), and the eight descended from (A), will have to be ranked as very distinct genera, or even as distinct sub-families.

Thus it is, as I believe, that two or more genera are produced by descent, with modification, from two or more species of the same genus. And the two or more parent-species are supposed to have descended from some one species of an earlier genus. In our diagram, this is indicated by the broken lines, beneath the capital letters, converging in sub-branches downwards towards a single point; this point representing a single species, the supposed single parent of our several new sub-genera and genera.

It is worthwhile to reflect for a moment on the character of the new species F14, which is supposed not to have diverged much in character, but to have retained the form of (F), either unaltered or altered only in a slight degree. In this case, its affinities to the other fourteen new species will be of a curious and circuitous nature. Having descended from a form which stood between the two parent-species (A) and (I), now supposed to be extinct and unknown, it will be in some degree intermediate in character between the two groups descended from these

species. But as these two groups have gone on diverging in character from the type of their parents, the new species (F14) will not be directly intermediate between them, but rather between types of the two groups; and every naturalist will be able to bring some such case before his mind.

In the diagram, each horizontal line has hitherto been supposed to represent a thousand generations, but each may represent a million or hundred million generations, and likewise a section of the successive strata of the earth's crust including extinct remains. We shall, when we come to our chapter on Geology, have to refer again to this subject, and I think we shall then see that the diagram throws light on the affinities of extinct beings, which, though generally belonging to the same orders, or families, or genera, with those now living, yet are often, in some degree, intermediate in character between existing groups; and we can understand this fact, for the extinct species lived at very ancient epochs when the branching lines of descent had diverged less.

I see no reason to limit the process of modification, as now explained, to the formation of genera alone. If, in our diagram, we suppose the amount of change represented by each successive group of diverging dotted lines to be very great, the forms marked a14 to p14, those marked b14 and f14, and those marked o14 to m14, will form three very distinct genera. We shall also have two very distinct genera descended from (I) and as these latter two genera, both from continued divergence of character and from inheritance from a different parent, will differ widely from the three genera descended from (A), the two little groups of genera will form two distinct families, or even orders, according to the amount of divergent modification supposed to be represented in the diagram. And the two new families, or orders, will have descended from two species of the original genus; and these two species are supposed to have descended from one species of a still more ancient and unknown genus.

We have seen that in each country it is the species of the larger genera which oftenest present varieties or incipient species. This, indeed, might have been expected; for as natural selection acts through one form having some advantage over other forms in the struggle for existence, it will chiefly act on those which already have some advantage; and the largeness of any group shows that its species have inherited from a common ancestor some advantage in common. Hence, the struggle for the production of new and modified descendants will mainly lie between the larger groups, which are all trying to increase in number. One large group will slowly conquer another large group, reduce its numbers, and thus lessen its chance of further variation and improvement. Within the same large group, the later and more highly perfected sub-groups, from branching out and seizing on many new places in the polity of Nature, will constantly tend to supplant and destroy the earlier and less improved sub-groups. Small and broken groups and sub-groups will finally tend to disappear. Looking to the future, we can predict that the groups of organic beings which are now large and triumphant, and which are least broken up, that is, which as yet have suffered least extinction, will for a long period continue to increase. But which groups will ultimately prevail, no man can predict; for we well know that many groups, formerly most extensively developed, have now become extinct. Looking still more remotely to the future, we may predict that, owing to the continued and steady increase of the larger groups, a multitude of smaller groups will become utterly extinct, and leave no modified descendants; and consequently that of the species living at any one period, extremely few will transmit descendants to a remote futurity. I shall have to return to this subject in the chapter on Classification, but I may add that on this view of extremely few of the more ancient species having transmitted descendants, and on the view of all the descendants of the same species making a class, we can understand how it is that there exist but very few classes in each main division of the animal and vegetable kingdoms. Although extremely few of the most ancient species may now have living and modified descendants, yet at the most remote geological period, the earth may have been as well peopled with many species of many genera, families, orders, and classes, as at the present day.

Summary of Chapter – If during the long course of ages and under varying conditions of life, organic beings vary at all in the several parts of their organisation, and I think this cannot be disputed; if there be, owing to the high geometrical powers of increase of each species, at some age, season, or year, a severe struggle for life, and this certainly cannot be disputed; then, considering the infinite complexity of the relations of all organic beings to each other and to their conditions of existence, causing an infinite diversity in structure, constitution, and habits, to be advantageous to them, I think it would be a most extraordinary fact if no variation ever had occurred useful to each being's own welfare, in the same way as so many variations have occurred useful to man. But if variations useful to any organic being do occur, assuredly individuals thus characterised will have the best chance of being preserved in the struggle for life; and from the strong principle of inheritance they will tend to produce offspring similarly characterised. This principle of preservation, I have called, for the sake of brevity, Natural Selection. Natural selection, on the principle of qualities being inherited at corresponding ages, can modify the egg, seed, or young, as easily as the adult. Amongst many animals, sexual selection will give its aid to ordinary selection, by assuring to the most vigorous and best-adapted males the greatest number of offspring. Sexual selection will also give characters useful to the males alone, in their struggles with other males.

Whether natural selection has really thus acted in nature, in modifying and adapting the various forms of life to their several conditions and stations, must be judged of by the general tenour and balance of evidence given in the following chapters. But we already see how it entails extinction; and how largely extinction has acted in the world's history, geology plainly declares. Natural selection, also, leads to divergence of character; for more living beings can be supported on the same area the more they diverge in structure, habits, and constitution, of which we see proof by looking at the inhabitants of any small spot or at naturalised productions. Therefore during the modification of the descendants of any one species, and during the incessant struggle of all species to increase in numbers, the more diversified these descendants become, the better will be their chance of succeeding in the battle of life. Thus the small differences distinguishing varieties of the same species, will steadily tend to increase till they come to equal the greater differences between species of the same genus, or even of distinct genera.

We have seen that it is the common, the widely-diffused, and widely-ranging species, belonging to the larger genera, which vary most; and these will tend to transmit to their modified offspring that superiority which now makes them dominant in their own countries. Natural selection, as has just been remarked, leads to divergence of character and to much extinction of the less improved and intermediate forms of life. On these principles, I believe, the nature of the affinities of all organic beings may be explained. It is a truly wonderful fact–the wonder of which we are apt to overlook from familiarity–that all animals and all plants throughout all time and space should be related to each other in group subordinate to group, in the manner which we everywhere behold–namely, varieties of the same species most closely related together, species of the same genus less closely and unequally related together, forming sections and sub-genera, species of distinct genera much less closely related, and genera related in different degrees, forming sub-families, families, orders, sub-classes, and classes. The several subordinate groups in any class cannot be ranked in a single file, but seem rather to be clustered round points, and these round other points, and so on in almost endless cycles. On the view that each species has been independently created, I can see no explanation of this great fact in the classification of all organic beings; but, to the best of my judgment, it is explained through inheritance and the complex action of natural selection, entailing extinction and divergence of character, as we have seen illustrated in the diagram.

The affinities of all the beings of the same class have sometimes been represented by a great tree. I believe this simile largely speaks the truth. The green and budding twigs may represent existing species; and those produced during each former year may represent the long

succession of extinct species. At each period of growth all the growing twigs have tried to branch out on all sides, and to overtop and kill the surrounding twigs and branches, in the same manner as species and groups of species have tried to overmaster other species in the great battle for life. The limbs divided into great branches, and these into lesser and lesser branches, were themselves once, when the tree was small, budding twigs; and this connexion of the former and present buds by ramifying branches may well represent the classification of all extinct and living species in groups subordinate to groups. Of the many twigs which flourished when the tree was a mere bush, only two or three, now grown into great branches, yet survive and bear all the other branches; so with the species which lived during long-past geological periods, very few now have living and modified descendants. From the first growth of the tree, many a limb and branch has decayed and dropped off; and these lost branches of various sizes may represent those whole orders, families, and genera which have now no living representatives, and which are known to us only from having been found in a fossil state. As we here and there see a thin straggling branch springing from a fork low down in a tree, and which by some chance has been favoured and is still alive on its summit, so we occasionally see an animal like the Ornithorhynchus or Lepidosiren, which in some small degree connects by its affinities two large branches of life, and which has apparently been saved from fatal competition by having inhabited a protected station. As buds give rise by growth to fresh buds, and these, if vigorous, branch out and overtop on all sides many a feebler branch, so by generation I believe it has been with the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever branching and beautiful ramifications.

Chapter XIV

Recapitulation and Conclusion

Recapitulation of the difficulties on the theory of Natural Selection – Recapitulation of the general and special circumstances in its favour – Causes of the general belief in the immutability of species – How far the theory of natural selection may be extended – Effects of its adoption on the study of Natural history – Concluding remarks.

As this whole volume is one long argument, it may be convenient to the reader to have the leading facts and inferences briefly recapitulated.

That many and grave objections may be advanced against the theory of descent with modification through natural selection, I do not deny. I have endeavoured to give to them their full force. Nothing at first can appear more difficult to believe than that the more complex organs and instincts should have been perfected, not by means superior to, though analogous with, human reason, but by the accumulation of innumerable slight variations, each good for the individual possessor. Nevertheless, this difficulty, though appearing to our imagination insuperably great, cannot be considered real if we admit the following propositions, namely, –that gradations in the perfection of any organ or instinct, which we may consider, either do now exist or could have existed, each good of its kind, –that all organs and instincts are, in ever so slight a degree, variable, –and, lastly, that there is a struggle for existence leading to the preservation of each profitable deviation of structure or instinct. The truth of these propositions cannot, I think, be disputed.

It is, no doubt, extremely difficult even to conjecture by what gradations many structures have been perfected, more especially amongst broken and failing groups of organic beings; but we see so many strange gradations in nature, as is proclaimed by the canon, 'Natura non facit saltum,' that we ought to be extremely cautious in saying that any organ or instinct, or any whole being, could not have arrived at its present state by many graduated steps. There are, it must be admitted, cases of special difficulty on the theory of natural selection; and one of the

most curious of these is the existence of two or three defined castes of workers or sterile females in the same community of ants; but I have attempted to show how this difficulty can be mastered.

With respect to the almost universal sterility of species when first crossed, which forms so remarkable a contrast with the almost universal fertility of varieties when crossed, I must refer the reader to the recapitulation of the facts given at the end of the eighth chapter, which seem to me conclusively to show that this sterility is no more a special endowment than is the incapacity of two trees to be grafted together, but that it is incidental on constitutional differences in the reproductive systems of the intercrossed species. We see the truth of this conclusion in the vast difference in the result, when the same two species are crossed reciprocally; that is, when one species is first used as the father and then as the mother.

The fertility of varieties when intercrossed and of their mongrel offspring cannot be considered as universal; nor is their very general fertility surprising when we remember that it is not likely that either their constitutions or their reproductive systems should have been profoundly modified. Moreover, most of the varieties which have been experimentised on have been produced under domestication; and as domestication apparently tends to eliminate sterility, we ought not to expect it also to produce sterility.

The sterility of hybrids is a very different case from that of first crosses, for their reproductive organs are more or less functionally impotent; whereas in first crosses the organs on both sides are in a perfect condition. As we continually see that organisms of all kinds are rendered in some degree sterile from their constitutions having been disturbed by slightly different and new conditions of life, we need not feel surprise at hybrids being in some degree sterile, for their constitutions can hardly fail to have been disturbed from being compounded of two distinct organisations. This parallelism is supported by another parallel, but directly opposite, class of facts; namely, that the vigour and fertility of all organic beings are increased by slight changes in their conditions of life, and that the offspring of slightly modified forms or varieties acquire from being crossed increased vigour and fertility. So that, on the one hand, considerable changes in the conditions of life and crosses between greatly modified forms, lessen fertility; and on the other hand, lesser changes in the conditions of life and crosses between less modified forms, increase fertility.

Turning to geographical distribution, the difficulties encountered on the theory of descent with modification are grave enough. All the individuals of the same species, and all the species of the same genus, or even higher group, must have descended from common parents; and therefore, in however distant and isolated parts of the world they are now found, they must in the course of successive generations have passed from some one part to the others. We are often wholly unable even to conjecture how this could have been affected. Yet, as we have reason to believe that some species have retained the same specific form for very long periods, enormously long as measured by years, too much stress ought not to be laid on the occasional wide diffusion of the same species; for during very long periods of time there will always be a good chance for wide migration by many means. A broken or interrupted range may often be accounted for by the extinction of the species in the intermediate regions. It cannot be denied that we are as yet very ignorant of the full extent of the various climatal and geographical changes which have affected the earth during modern periods; and such changes will obviously have greatly facilitated migration. As an example, I have attempted to show how potent has been the influence of the Glacial period on the distribution both of the same and of representative species throughout the world. We are as yet profoundly ignorant of the many occasional means of transport. With respect to distinct species of the same genus inhabiting very distant and isolated regions, as the process of modification has necessarily been slow, all the means of migration will have been possible during a very long period; and consequently the difficulty of the wide diffusion of species of the same genus is in some degree lessened.

As on the theory of natural selection an interminable number of intermediate forms must have existed, linking together all the species in each group by gradations as fine as our present varieties, it may be asked, Why do we not see these linking forms all around us? Why are not all organic beings blended together in an inextricable chaos? With respect to existing forms, we should remember that we have no right to expect (excepting in rare cases) to discover directly connecting links between them, but only between each and some extinct and supplanted form. Even on a wide area, which has during a long period remained continuous, and of which the climate and other conditions of life change insensibly in going from a district occupied by one species into another district occupied by a closely allied species, we have no just right to expect often to find intermediate varieties in the intermediate zone. For we have reason to believe that only a few species are undergoing change at any one period; and all changes are slowly effected. I have also shown that the intermediate varieties which will at first probably exist in the intermediate zones, will be liable to be supplanted by the allied forms on either hand; and the latter, from existing in greater numbers, will generally be modified and improved at a quicker rate than the intermediate varieties, which exist in lesser numbers; so that the intermediate varieties will, in the long run, be supplanted and exterminated.

On this doctrine of the extermination of an infinitude of connecting links, between the living and extinct inhabitants of the world, and at each successive period between the extinct and still older species, why is not every geological formation charged with such links? Why does not every collection of fossil remains afford plain evidence of the gradation and mutation of the forms of life? We meet with no such evidence, and this is the most obvious and forcible of the many objections which may be urged against my theory. Why, again, do whole groups of allied species appear, though certainly they often falsely appear, to have come in suddenly on the several geological stages? Why do we not find great piles of strata beneath the Silurian system, stored with the remains of the progenitors of the Silurian groups of fossils? For certainly on my theory such strata must somewhere have been deposited at these ancient and utterly unknown epochs in the world's history.

I can answer these questions and grave objections only on the supposition that the geological record is far more imperfect than most geologists believe. It cannot be objected that there has not been time sufficient for any amount of organic change; for the lapse of time has been so great as to be utterly inappreciable by the human intellect. The number of specimens in all our museums is absolutely as nothing compared with the countless generations of countless species which certainly have existed. We should not be able to recognise a species as the parent of any one or more species if we were to examine them ever so closely, unless we likewise possessed many of the intermediate links between their past or parent and present states; and these many links we could hardly ever expect to discover, owing to the imperfection of the geological record. Numerous existing doubtful forms could be named which are probably varieties; but who will pretend that in future ages so many fossil links will be discovered, that naturalists will be able to decide, on the common view, whether or not these doubtful forms are varieties? As long as most of the links between any two species are unknown, if any one link or intermediate variety be discovered, it will simply be classed as another and distinct species. Only a small portion of the world has been geologically explored. Only organic beings of certain classes can be preserved in a fossil condition, at least in any great number. Widely ranging species vary most, and varieties are often at first local, –both causes rendering the discovery of intermediate links less likely. Local varieties will not spread into other and distant regions until they are considerably modified and improved; and when they do spread, if discovered in a geological formation, they will appear as if suddenly created there, and will be simply classed as new species. Most formations have been intermittent in their accumulation; and their duration, I am inclined to believe, has been shorter than the average duration of specific forms. Successive formations are separated from each other by enormous blank intervals of time; for fossiliferous formations, thick enough to resist

future degradation, can be accumulated only where much sediment is deposited on the subsiding bed of the sea. During the alternate periods of elevation and of stationary level the record will be blank. During these latter periods there will probably be more variability in the forms of life; during periods of subsidence, more extinction.

With respect to the absence of fossiliferous formations beneath the lowest Silurian strata, I can only recur to the hypothesis given in the ninth chapter. That the geological record is imperfect all will admit; but that it is imperfect to the degree which I require, few will be inclined to admit. If we look to long enough intervals of time, geology plainly declares that all species have changed; and they have changed in the manner which my theory requires, for they have changed slowly and in a graduated manner. We clearly see this in the fossil remains from consecutive formations invariably being much more closely related to each other, than are the fossils from formations distant from each other in time.

Such is the sum of the several chief objections and difficulties which may justly be urged against my theory; and I have now briefly recapitulated the answers and explanations which can be given to them. I have felt these difficulties far too heavily during many years to doubt their weight. But it deserves especial notice that the more important objections relate to questions on which we are not confessedly ignorant; nor do we know how ignorant we are. We do not know all the possible transitional gradations between the simplest and the most perfect organs; it cannot be pretended that we know all the varied means of Distribution during the long lapse of years, or that we know how imperfect the Geological Record is. Grave as these several difficulties are, in my judgment they do not overthrow the theory of descent with modification.

Now let us turn to the other side of the argument. Under domestication we see much variability. This seems to be mainly due to the reproductive system being eminently susceptible to changes in the conditions of life; so that this system, when not rendered impotent, fails to reproduce offspring exactly like the parent-form. Variability is governed by many complex laws, –by correlation of growth, by use and disuse, and by the direct action of the physical conditions of life. There is much difficulty in ascertaining how much modification our domestic productions have undergone; but we may safely infer that the amount has been large, and that modifications can be inherited for long periods. As long as the conditions of life remain the same, we have reason to believe that a modification, which has already been inherited for many generations, may continue to be inherited for an almost infinite number of generations. On the other hand we have evidence that variability, when it has once come into play, does not wholly cease; for new varieties are still occasionally produced by our most anciently domesticated productions.

Man does not actually produce variability; he only unintentionally exposes organic beings to new conditions of life, and then nature acts on the organisation, and causes variability. But man can and does select the variations given to him by nature, and thus accumulate them in any desired manner. He thus adapts animals and plants for his own benefit or pleasure. He may do this methodically, or he may do it unconsciously by preserving the individuals most useful to him at the time, without any thought of altering the breed. It is certain that he can largely influence the character of a breed by selecting, in each successive generation, individual differences so slight as to be quite inappreciable by an uneducated eye. This process of selection has been the great agency in the production of the most distinct and useful domestic breeds. That many of the breeds produced by man have to a large extent the character of natural species, is shown by the inextricable doubts whether very many of them are varieties or aboriginal species.

There is no obvious reason why the principles which have acted so efficiently under domestication should not have acted under nature. In the preservation of favoured individuals and races, during the constantly-recurrent Struggle for Existence, we see the most powerful and ever-acting means of selection. The struggle for existence inevitably follows from the high

geometrical ratio of increase which is common to all organic beings. This high rate of increase is proved by calculation, by the effects of a succession of peculiar seasons, and by the results of naturalisation, as explained in the third chapter. More individuals are born than can possibly survive. A grain in the balance will determine which individual shall live and which shall die, –which variety or species shall increase in number, and which shall decrease, or finally become extinct. As the individuals of the same species come in all respects into the closest competition with each other, the struggle will generally be most severe between them; it will be almost equally severe between the varieties of the same species, and next in severity between the species of the same genus. But the struggle will often be very severe between beings most remote in the scale of nature. The slightest advantage in one being, at any age or during any season, over those with which it comes into competition, or better adaptation in however slight a degree to the surrounding physical conditions, will turn the balance.

With animals having separated sexes there will in most cases be a struggle between the males for possession of the females. The most vigorous individuals, or those which have most successfully struggled with their conditions of life, will generally leave most progeny. But success will often depend on having special weapons or means of defence, or on the charms of the males; and the slightest advantage will lead to victory.

As geology plainly proclaims that each land has undergone great physical changes, we might have expected that organic beings would have varied under nature, in the same way as they generally have varied under the changed conditions of domestication. And if there be any variability under nature, it would be an unaccountable fact if natural selection had not come into play. It has often been asserted, but the assertion is quite incapable of proof, that the amount of variation under nature is a strictly limited quantity. Man, though acting on external characters alone and often capriciously, can produce within a short period a great result by adding up mere individual differences in his domestic productions; and every one admits that there are at least individual differences in species under nature. But, besides such differences, all naturalists have admitted the existence of varieties, which they think sufficiently distinct to be worthy of record in systematic works. No one can draw any clear distinction between individual differences and slight varieties; or between more plainly marked varieties and sub-species, and species. Let it be observed how naturalists differ in the rank which they assign to the many representative forms in Europe and North America.

If then we have under nature variability and a powerful agent always ready to act and select, why should we doubt that variations in any way useful to beings, under their excessively complex relations of life, would be preserved, accumulated, and inherited? Why, if man can by patience select variations most useful to himself, should nature fail in selecting variations useful, under changing conditions of life, to her living products? What limit can be put to this power, acting during long ages and rigidly scrutinising the whole constitution, structure, and habits of each creature, –favouring the good and rejecting the bad? I can see no limit to this power, in slowly and beautifully adapting each form to the most complex relations of life. The theory of natural selection, even if we looked no further than this, seems to me to be in itself probable. I have already recapitulated, as fairly as I could, the opposed difficulties and objections: now let us turn to the special facts and arguments in favour of the theory.

On the view that species are only strongly marked and permanent varieties, and that each species first existed as a variety, we can see why it is that no line of demarcation can be drawn between species, commonly supposed to have been produced by special acts of creation, and varieties which are acknowledged to have been produced by secondary laws. On this same view we can understand how it is that in each region where many species of a genus have been produced, and where they now flourish, these same species should present many varieties; for where the manufactory of species has been active, we might expect, as a general rule, to find it still in action; and this is the case if varieties be incipient species. Moreover, the species of the large genera, which afford the greater number of varieties or incipient species, retain to a

certain degree the character of varieties; for they differ from each other by a less amount of difference than do the species of smaller genera. The closely allied species also of the larger genera apparently have restricted ranges, and they are clustered in little groups round other species–in which respects they resemble varieties. These are strange relations on the view of each species having been independently created, but are intelligible if all species first existed as varieties.

As each species tends by its geometrical ratio of reproduction to increase inordinately in number; and as the modified descendants of each species will be enabled to increase by so much the more as they become more diversified in habits and structure, so as to be enabled to seize on many and widely different places in the economy of nature, there will be a constant tendency in natural selection to preserve the most divergent offspring of any one species. Hence during a long-continued course of modification, the slight differences, characteristic of varieties of the same species, tend to be augmented into the greater differences characteristic of species of the same genus. New and improved varieties will inevitably supplant and exterminate the older, less improved and intermediate varieties; and thus species are rendered to a large extent defined and distinct objects. Dominant species belonging to the larger groups tend to give birth to new and dominant forms; so that each large group tends to become still larger, and at the same time more divergent in character. But as all groups cannot thus succeed in increasing in size, for the world would not hold them, the more dominant groups beat the less dominant. This tendency in the large groups to go on increasing in size and diverging in character, together with the almost inevitable contingency of much extinction, explains the arrangement of all the forms of life, in groups subordinate to groups, all within a few great classes, which we now see everywhere around us, and which has prevailed throughout all time. This grand fact of the grouping of all organic beings seems to me utterly inexplicable on the theory of creation.

As natural selection acts solely by accumulating slight, successive, favourable variations, it can produce no great or sudden modification; it can act only by very short and slow steps. Hence the canon of 'Natura non facit saltum,' which every fresh addition to our knowledge tends to make more strictly correct, is on this theory simply intelligible. We can plainly see why nature is prodigal in variety, though niggard in innovation. But why this should be a law of nature if each species has been independently created, no man can explain.

Many other facts are, as it seems to me, explicable on this theory. How strange it is that a bird, under the form of woodpecker, should have been created to prey on insects on the ground; that upland geese, which never or rarely swim, should have been created with webbed feet; that a thrush should have been created to dive and feed on sub-aquatic insects; and that a petrel should have been created with habits and structure fitting it for the life of an auk or grebe! And so on in endless other cases. But on the view of each species constantly trying to increase in number, with natural selection always ready to adapt the slowly varying descendants of each to any unoccupied or ill-occupied place in nature, these facts cease to be strange, or perhaps might even have been anticipated.

As natural selection acts by competition, it adapts the inhabitants of each country only in relation to the degree of perfection of their associates; so that we need feel no surprise at the inhabitants of any one country, although on the ordinary view supposed to have been specially created and adapted for that country, being beaten and supplanted by the naturalised productions from another land. Nor ought we to marvel if all the contrivances in nature be not, as far as we can judge, absolutely perfect; and if some of them be abhorrent to our ideas of fitness. We need not marvel at the sting of the bee causing the bee's own death; at drones being produced in such vast numbers for one single act, and being then slaughtered by their sterile sisters; at the astonishing waste of pollen by our fir-trees; at the instinctive hatred of the queen bee for her own fertile daughters; at ichneumonidae feeding within the live bodies of

caterpillars; and at other such cases. The wonder indeed is, on the theory of natural selection, that more cases of the want of absolute perfection have not been observed.

The complex and little known laws governing variation are the same, as far as we can see, with the laws which have governed the production of so-called specific forms. In both cases physical conditions seem to have produced but little direct effect; yet when varieties enter any zone, they occasionally assume some of the characters of the species proper to that zone. In both varieties and species, use and disuse seem to have produced some effect; for it is difficult to resist this conclusion when we look, for instance, at the logger-headed duck, which has wings incapable of flight, in nearly the same condition as in the domestic duck; or when we look at the burrowing tucutucu, which is occasionally blind, and then at certain moles, which are habitually blind and have their eyes covered with skin; or when we look at the blind animals inhabiting the dark caves of America and Europe. In both varieties and species correlation of growth seems to have played a most important part, so that when one part has been modified other parts are necessarily modified. In both varieties and species reversions to long-lost characters occur. How inexplicable on the theory of creation is the occasional appearance of stripes on the shoulder and legs of the several species of the horse-genus and in their hybrids! How simply is this fact explained if we believe that these species have descended from a striped progenitor, in the same manner as the several domestic breeds of pigeon have descended from the blue and barred rock-pigeon!

On the ordinary view of each species having been independently created, why should the specific characters, or those by which the species of the same genus differ from each other, be more variable than the generic characters in which they all agree? Why, for instance, should the colour of a flower be more likely to vary in any one species of a genus, if the other species, supposed to have been created independently, have differently coloured flowers, than if all the species of the genus have the same coloured flowers? If species are only well-marked varieties, of which the characters have become in a high degree permanent, we can understand this fact; for they have already varied since they branched off from a common progenitor in certain characters, by which they have come to be specifically distinct from each other; and therefore these same characters would be more likely still to be variable than the generic characters which have been inherited without change for an enormous period. It is inexplicable on the theory of creation why a part developed in a very unusual manner in any one species of a genus, and therefore, as we may naturally infer, of great importance to the species, should be eminently liable to variation; but, on my view, this part has undergone, since the several species branched off from a common progenitor, an unusual amount of variability and modification, and therefore we might expect this part generally to be still variable. But a part may be developed in the most unusual manner, like the wing of a bat, and yet not be more variable than any other structure, if the part be common to many subordinate forms, that is, if it has been inherited for a very long period; for in this case it will have been rendered constant by long-continued natural selection.

Glancing at instincts, marvellous as some are, they offer no greater difficulty than does corporeal structure on the theory of the natural selection of successive, slight, but profitable modifications. We can thus understand why nature moves by graduated steps in endowing different animals of the same class with their several instincts. I have attempted to show how much light the principle of gradation throws on the admirable architectural powers of the hive-bee. Habit no doubt sometimes comes into play in modifying instincts; but it certainly is not indispensable, as we see, in the case of neuter insects, which leave no progeny to inherit the effects of long-continued habit. On the view of all the species of the same genus having descended from a common parent, and having inherited much in common, we can understand how it is that allied species, when placed under considerably different conditions of life, yet should follow nearly the same instincts; why the thrush of South America, for instance, lines her nest with mud like our British species. On the view of instincts having been slowly

acquired through natural selection we need not marvel at some instincts being apparently not perfect and liable to mistakes, and at many instincts causing other animals to suffer.

If species be only well-marked and permanent varieties, we can at once see why their crossed offspring should follow the same complex laws in their degrees and kinds of resemblance to their parents, –in being absorbed into each other by successive crosses, and in other such points, –as do the crossed offspring of acknowledged varieties. On the other hand, these would be strange facts if species have been independently created, and varieties have been produced by secondary laws.

If we admit that the geological record is imperfect in an extreme degree, then such facts as the record gives support the theory of descent with modification. New species have come on the stage slowly and at successive intervals; and the amount of change, after equal intervals of time, is widely different in different groups. The extinction of species and of whole groups of species, which has played so conspicuous a part in the history of the organic world, almost inevitably follows on the principle of natural selection; for old forms will be supplanted by new and improved forms. Neither single species nor groups of species reappear when the chain of ordinary generation has once been broken. The gradual diffusion of dominant forms, with the slow modification of their descendants, causes the forms of life, after long intervals of time, to appear as if they had changed simultaneously throughout the world. The fact of the fossil remains of each formation being in some degree intermediate in character between the fossils in the formations above and below, is simply explained by their intermediate position in the chain of descent. The grand fact that all extinct organic beings belong to the same system with recent beings, falling either into the same or into intermediate groups, follows from the living and the extinct being the offspring of common parents. As the groups which have descended from an ancient progenitor have generally diverged in character, the progenitor with its early descendants will often be intermediate in character in comparison with its later descendants; and thus we can see why the more ancient a fossil is, the oftener it stands in some degree intermediate between existing and allied groups. Recent forms are generally looked at as being, in some vague sense, higher than ancient and extinct forms; and they are in so far higher as the later and more improved forms have conquered the older and less improved organic beings in the struggle for life. Lastly, the law of the long endurance of allied forms on the same continent, –of marsupials in Australia, of edentata in America, and other such cases, –is intelligible, for within a confined country, the recent and the extinct will naturally be allied by descent.

Looking to geographical distribution, if we admit that there has been during the long course of ages much migration from one part of the world to another, owing to former climatal and geographical changes and to the many occasional and unknown means of dispersal, then we can understand, on the theory of descent with modification, most of the great leading facts in Distribution. We can see why there should be so striking a parallelism in the distribution of organic beings throughout space, and in their geological succession throughout time; for in both cases the beings have been connected by the bond of ordinary generation, and the means of modification have been the same. We see the full meaning of the wonderful fact, which must have struck every traveller, namely, that on the same continent, under the most diverse conditions, under heat and cold, on mountain and lowland, on deserts and marshes, most of the inhabitants within each great class are plainly related; for they will generally be descendants of the same progenitors and early colonists. On this same principle of former migration, combined in most cases with modification, we can understand, by the aid of the Glacial period, the identity of some few plants, and the close alliance of many others, on the most distant mountains, under the most different climates; and likewise the close alliance of some of the inhabitants of the sea in the northern and southern temperate zones, though separated by the whole intertropical ocean. Although two areas may present the same physical conditions of life, we need feel no surprise at their inhabitants being widely different, if they have been for a

long period completely separated from each other; for as the relation of organism to organism is the most important of all relations, and as the two areas will have received colonists from some third source or from each other, at various periods and in different proportions, the course of modification in the two areas will inevitably be different.

On this view of migration, with subsequent modification, we can see why oceanic islands should be inhabited by few species, but of these, that many should be peculiar. We can clearly see why those animals which cannot cross wide spaces of ocean, as frogs and terrestrial mammals, should not inhabit oceanic islands; and why, on the other hand, new and peculiar species of bats, which can traverse the ocean, should so often be found on islands far distant from any continent. Such facts as the presence of peculiar species of bats, and the absence of all other mammals, on oceanic islands, are utterly inexplicable on the theory of independent acts of creation.

The existence of closely allied or representative species in any two areas, implies, on the theory of descent with modification, that the same parents formerly inhabited both areas; and we almost invariably find that wherever many closely allied species inhabit two areas, some identical species common to both still exist. Wherever many closely allied yet distinct species occur, many doubtful forms and varieties of the same species likewise occur. It is a rule of high generality that the inhabitants of each area are related to the inhabitants of the nearest source whence immigrants might have been derived. We see this in nearly all the plants and animals of the Galapagos archipelago, of Juan Fernandez, and of the other American islands being related in the most striking manner to the plants and animals of the neighbouring American mainland; and those of the Cape de Verde archipelago and other African islands to the African mainland. It must be admitted that these facts receive no explanation on the theory of creation.

The fact, as we have seen, that all past and present organic beings constitute one grand natural system, with group subordinate to group, and with extinct groups often falling in between recent groups, is intelligible on the theory of natural selection with its contingencies of extinction and divergence of character. On these same principles we see how it is, that the mutual affinities of the species and genera within each class are so complex and circuitous. We see why certain characters are far more serviceable than others for classification; –why adaptive characters, though of paramount importance to the being, are of hardly any importance in classification; why characters derived from rudimentary parts, though of no service to the being, are often of high classificatory value; and why embryological characters are the most valuable of all. The real affinities of all organic beings are due to inheritance or community of descent. The natural system is a genealogical arrangement, in which we have to discover the lines of descent by the most permanent characters, however slight their vital importance may be.

The framework of bones being the same in the hand of a man, wing of a bat, fin of the porpoise, and leg of the horse, –the same number of vertebrae forming the neck of the giraffe and of the elephant, –and innumerable other such facts, at once explain themselves on the theory of descent with slow and slight successive modifications. The similarity of pattern in the wing and leg of a bat, though used for such different purpose, –in the jaws and legs of a crab, –in the petals, stamens, and pistils of a flower, is likewise intelligible on the view of the gradual modification of parts or organs, which were alike in the early progenitor of each class. On the principle of successive variations not always supervening at an early age, and being inherited at a corresponding not early period of life, we can clearly see why the embryos of mammals, birds, reptiles, and fishes should be so closely alike, and should be so unlike the adult forms. We may cease marvelling at the embryo of an air-breathing mammal or bird having branchial slits and arteries running in loops, like those in a fish which has to breathe the air dissolved in water, by the aid of well-developed branchiae.

Disuse, aided sometimes by natural selection, will often tend to reduce an organ, when it has become useless by changed habits or under changed conditions of life; and we can clearly understand on this view the meaning of rudimentary organs. But disuse and selection will generally act on each creature, when it has come to maturity and has to play its full part in the struggle for existence, and will thus have little power of acting on an organ during early life; hence the organ will not be much reduced or rendered rudimentary at this early age. The calf, for instance, has inherited teeth, which never cut through the gums of the upper jaw, from an early progenitor having well-developed teeth; and we may believe, that the teeth in the mature animal were reduced, during successive generations, by disuse or by the tongue and palate having been fitted by natural selection to browse without their aid; whereas in the calf, the teeth have been left untouched by selection or disuse, and on the principle of inheritance at corresponding ages have been inherited from a remote period to the present day. On the view of each organic being and each separate organ having been specially created, how utterly inexplicable it is that parts, like the teeth in the embryonic calf or like the shrivelled wings under the soldered wing-covers of some beetles, should thus so frequently bear the plain stamp of inutility! Nature may be said to have taken pains to reveal, by rudimentary organs and by homologous structures, her scheme of modification, which it seems that we wilfully will not understand.

I have now recapitulated the chief facts and considerations which have thoroughly convinced me that species have changed, and are still slowly changing by the preservation and accumulation of successive slight favourable variations. Why, it may be asked, have all the most eminent living naturalists and geologists rejected this view of the mutability of species? It cannot be asserted that organic beings in a state of nature are subject to no variation; it cannot be proved that the amount of variation in the course of long ages is a limited quantity; no clear distinction has been, or can be, drawn between species and well-marked varieties. It cannot be maintained that species when intercrossed are invariably sterile, and varieties invariably fertile; or that sterility is a special endowment and sign of creation. The belief that species were immutable productions was almost unavoidable as long as the history of the world was thought to be of short duration; and now that we have acquired some idea of the lapse of time, we are too apt to assume, without proof, that the geological record is so perfect that it would have afforded us plain evidence of the mutation of species, if they had undergone mutation.

But the chief cause of our natural unwillingness to admit that one species has given birth to other and distinct species, is that we are always slow in admitting any great change of which we do not see the intermediate steps. The difficulty is the same as that felt by so many geologists, when Lyell first insisted that long lines of inland cliffs had been formed, and great valleys excavated, by the slow action of the coast-waves. The mind cannot possibly grasp the full meaning of the term of a hundred million years; it cannot add up and perceive the full effects of many slight variations, accumulated during an almost infinite number of generations.

Although I am fully convinced of the truth of the views given in this volume under the form of an abstract, I by no means expect to convince experienced naturalists whose minds are stocked with a multitude of facts all viewed, during a long course of years, from a point of view directly opposite to mine. It is so easy to hide our ignorance under such expressions as the 'plan of creation,' 'unity of design,' &c., and to think that we give an explanation when we only restate a fact. Any one whose disposition leads him to attach more weight to unexplained difficulties than to the explanation of a certain number of facts will certainly reject my theory. A few naturalists, endowed with much flexibility of mind, and who have already begun to doubt on the immutability of species, may be influenced by this volume; but I look with confidence to the future, to young and rising naturalists, who will be able to view both sides of the question with impartiality. Whoever is led to believe that species are mutable will do good

service by conscientiously expressing his conviction; for only thus can the load of prejudice by which this subject is overwhelmed be removed.

Several eminent naturalists have of late published their belief that a multitude of reputed species in each genus are not real species; but that other species are real, that is, have been independently created. This seems to me a strange conclusion to arrive at. They admit that a multitude of forms, which till lately they themselves thought were special creations, and which are still thus looked at by the majority of naturalists, and which consequently have every external characteristic feature of true species, –they admit that these have been produced by variation, but they refuse to extend the same view to other and very slightly different forms. Nevertheless they do not pretend that they can define, or even conjecture, which are the created forms of life, and which are those produced by secondary laws. They admit variation as a vera causa in one case, they arbitrarily reject it in another, without assigning any distinction in the two cases. The day will come when this will be given as a curious illustration of the blindness of preconceived opinion. These authors seem no more startled at a miraculous act of creation than at an ordinary birth. But do they really believe that at innumerable periods in the earth's history certain elemental atoms have been commanded suddenly to flash into living tissues? Do they believe that at each supposed act of creation one individual or many were produced? Were all the infinitely numerous kinds of animals and plants created as eggs or seed, or as full grown? And in the case of mammals, were they created bearing the false marks of nourishment from the mother's womb? Although naturalists very properly demand a full explanation of every difficulty from those who believe in the mutability of species, on their own side they ignore the whole subject of the first appearance of species in what they consider reverent silence.

It may be asked how far I extend the doctrine of the modification of species. The question is difficult to answer, because the more distinct the forms are which we may consider, by so much the arguments fall away in force. But some arguments of the greatest weight extend very far. All the members of whole classes can be connected together by chains of affinities, and all can be classified on the same principle, in groups subordinate to groups. Fossil remains sometimes tend to fill up very wide intervals between existing orders. Organs in a rudimentary condition plainly show that an early progenitor had the organ in a fully developed state; and this in some instances necessarily implies an enormous amount of modification in the descendants. Throughout whole classes various structures are formed on the same pattern, and at an embryonic age the species closely resemble each other. Therefore I cannot doubt that the theory of descent with modification embraces all the members of the same class. I believe that animals have descended from at most only four or five progenitors, and plants from an equal or lesser number.

Analogy would lead me one step further, namely, to the belief that all animals and plants have descended from some one prototype. But analogy may be a deceitful guide. Nevertheless all living things have much in common, in their chemical composition, their germinal vesicles, their cellular structure, and their laws of growth and reproduction. We see this even in so trifling a circumstance as that the same poison often similarly affects plants and animals; or that the poison secreted by the gall-fly produces monstrous growths on the wild rose or oak-tree. Therefore I should infer from analogy that probably all the organic beings which have ever lived on this earth have descended from some one primordial form, into which life was first breathed.

When the views entertained in this volume on the origin of species, or when analogous views are generally admitted, we can dimly foresee that there will be a considerable revolution in natural history. Systematists will be able to pursue their labours as at present; but they will not be incessantly haunted by the shadowy doubt whether this or that form be in essence a species. This I feel sure, and I speak after experience, will be no slight relief. The endless disputes whether or not some fifty species of British brambles are true species will cease.

Systematists will have only to decide (not that this will be easy) whether any form be sufficiently constant and distinct from other forms, to be capable of definition; and if definable, whether the differences be sufficiently important to deserve a specific name. This latter point will become a far more essential consideration than it is at present; for differences, however slight, between any two forms, if not blended by intermediate gradations, are looked at by most naturalists as sufficient to raise both forms to the rank of species. Hereafter we shall be compelled to acknowledge that the only distinction between species and well-marked varieties is, that the latter are known, or believed, to be connected at the present day by intermediate gradations, whereas species were formerly thus connected. Hence, without quite rejecting the consideration of the present existence of intermediate gradations between any two forms, we shall be led to weigh more carefully and to value higher the actual amount of difference between them. It is quite possible that forms now generally acknowledged to be merely varieties may hereafter be thought worthy of specific names, as with the primrose and cowslip; and in this case scientific and common language will come into accordance. In short, we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect; but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species.

The other and more general departments of natural history will rise greatly in interest. The terms used by naturalists of affinity, relationship, community of type, paternity, morphology, adaptive characters, rudimentary and aborted organs, &c., will cease to be metaphorical, and will have a plain signification. When we no longer look at an organic being as a savage looks at a ship, as at something wholly beyond his comprehension; when we regard every production of nature as one which has had a history; when we contemplate every complex structure and instinct as the summing up of many contrivances, each useful to the possessor, nearly in the same way as when we look at any great mechanical invention as the summing up of the labour, the experience, the reason, and even the blunders of numerous workmen; when we thus view each organic being, how far more interesting, I speak from experience, will the study of natural history become!

A grand and almost untrodden field of inquiry will be opened, on the causes and laws of variation, on correlation of growth, on the effects of use and disuse, on the direct action of external conditions, and so forth. The study of domestic productions will rise immensely in value. A new variety raised by man will be a far more important and interesting subject for study than one more species added to the infinitude of already recorded species. Our classifications will come to be, as far as they can be so made, genealogies; and will then truly give what may be called the plan of creation. The rules for classifying will no doubt become simpler when we have a definite object in view. We possess no pedigrees or armorial bearings; and we have to discover and trace the many diverging lines of descent in our natural genealogies, by characters of any kind which have long been inherited. Rudimentary organs will speak infallibly with respect to the nature of long-lost structures. Species and groups of species, which are called aberrant, and which may fancifully be called living fossils, will aid us in forming a picture of the ancient forms of life. Embryology will reveal to us the structure, in some degree obscured, of the prototypes of each great class.

When we can feel assured that all the individuals of the same species, and all the closely allied species of most genera, have within a not very remote period descended from one parent, and have migrated from some one birthplace; and when we better know the many means of migration, then, by the light which geology now throws, and will continue to throw, on former changes of climate and of the level of the land, we shall surely be enabled to trace in an admirable manner the former migrations of the inhabitants of the whole world. Even at present, by comparing the differences of the inhabitants of the sea on the opposite sides of a

continent, and the nature of the various inhabitants of that continent in relation to their apparent means of immigration, some light can be thrown on ancient geography.

The noble science of Geology loses glory from the extreme imperfection of the record. The crust of the earth with its embedded remains must not be looked at as a well-filled museum, but as a poor collection made at hazard and at rare intervals. The accumulation of each great fossiliferous formation will be recognised as having depended on an unusual concurrence of circumstances, and the blank intervals between the successive stages as having been of vast duration. But we shall be able to gauge with some security the duration of these intervals by a comparison of the preceding and succeeding organic forms. We must be cautious in attempting to correlate as strictly contemporaneous two formations, which include few identical species, by the general succession of their forms of life. As species are produced and exterminated by slowly acting and still existing causes, and not by miraculous acts of creation and by catastrophes; and as the most important of all causes of organic change is one which is almost independent of altered and perhaps suddenly altered physical conditions, namely, the mutual relation of organism to organism, –the improvement of one being entailing the improvement or the extermination of others; it follows, that the amount of organic change in the fossils of consecutive formations probably serves as a fair measure of the lapse of actual time. A number of species, however, keeping in a body might remain for a long period unchanged, whilst within this same period, several of these species, by migrating into new countries and coming into competition with foreign associates, might become modified; so that we must not overrate the accuracy of organic change as a measure of time. During early periods of the earth's history, when the forms of life were probably fewer and simpler, the rate of change was probably slower; and at the first dawn of life, when very few forms of the simplest structure existed, the rate of change may have been slow in an extreme degree. The whole history of the world, as at present known, although of a length quite incomprehensible by us, will hereafter be recognised as a mere fragment of time, compared with the ages which have elapsed since the first creature, the progenitor of innumerable extinct and living descendants, was created.

In the distant future I see open fields for far more important researches. Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation. Light will be thrown on the origin of man and his history.

Authors of the highest eminence seem to be fully satisfied with the view that each species has been independently created. To my mind it accords better with what we know of the laws impressed on matter by the Creator, that the production and extinction of the past and present inhabitants of the world should have been due to secondary causes, like those determining the birth and death of the individual. When I view all beings not as special creations, but as the lineal descendants of some few beings which lived long before the first bed of the Silurian system was deposited, they seem to me to become ennobled. Judging from the past, we may safely infer that not one living species will transmit its unaltered likeness to a distant futurity. And of the species now living very few will transmit progeny of any kind to a far distant futurity; for the manner in which all organic beings are grouped, shows that the greater number of species of each genus, and all the species of many genera, have left no descendants, but have become utterly extinct. We can so far take a prophetic glance into futurity as to foretel that it will be the common and widely-spread species, belonging to the larger and dominant groups, which will ultimately prevail and procreate new and dominant species. As all the living forms of life are the lineal descendants of those which lived long before the Silurian epoch, we may feel certain that the ordinary succession by generation has never once been broken, and that no cataclysm has desolated the whole world. Hence we may look with some confidence to a secure future of equally inappreciable length. And as natural selection works solely by and for

the good of each being, all corporeal and mental endowments will tend to progress towards perfection.

It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us. These laws, taken in the largest sense, being Growth with Reproduction; Inheritance which is almost implied by reproduction; Variability from the indirect and direct action of the external conditions of life, and from use and disuse; a Ratio of Increase so high as to lead to a Struggle for Life, and as a consequence to Natural Selection, entailing Divergence of Character and the Extinction of less-improved forms. Thus, from the war of nature, from famine and death, the most exalted object, that we are capable of conceiving, namely, the production of the higher animals directly follows. There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.

Questions to guide you towards an understanding of the Origin of Species*:*

I. Darwin's Introduction to The Origin.

A. What specific kinds of evidence does Darwin suggest must lead to an acceptance of the transmutability of species?

B. Why does Darwin's theory suggest a monophyletic and not a polyphyletic origin of species?

II. Chapter 3, Struggle for Existence.

A. What is Darwin's Struggle for existence?

B. How does Darwin equate the struggle for existence with an organism's adaptation to the environment?

C. Who was Thomas Malthus and what is a geometric rate of increase?

III. Chapter 4, Natural Selection.

A. How does Darwin explain natural selection?

B. Compare natural selection to artificial selection?

C. What is sexual selection and how does it differ from natural selection?

D. Can you interpret the diagram Darwin uses to illustrate character divergence and descent from a common ancestor? What does it illustrate in regards to divergence and extinction?

E. How do Darwin and Lamarck differ concerning the problem of progression of form?

ALFRED WALLACE

On the Tendency of Varieties to Depart Indefinitely from the Original Type (1859)

Alfred Russel Wallace (1823–1913) was a surveyor with a passion for investigating nature. Despite his lack of formal training, he traveled to the upper reaches of the Amazon in search of clues to the "origin of species" (a term he used in 1847). He supported himself by providing museums with wildlife specimens. Then he sailed to the East Indies where he continued collecting biological specimens. By 1858 he was second to no one in his detailed understanding of the relation between species and environment.

While he was in Ternate, one of the spice islands in what is now Indonesia, Wallace suffered from malaria. During an attack of fever, he suddenly understood the relationship between the struggle to survive and the evolution of species. He quickly wrote the following essay and mailed it to England. Three months later it reached its addressee, Charles Darwin, who was thunderstruck. Here, in excellent prose, was the theory he had struggled over for decades. Fortunately for Darwin, Wallace was all curiosity and no personal ambition. Wallace agreed that Darwin should be credited with the idea, and when he published his own book about evolution, he even titled it *Darwinism* (1889). Darwin is now famous around the world, whereas Alfred Wallace is remembered only by specialists. Yet Wallace's essay still shines with its clear outline of the process of natural selection.

One of the strongest arguments which have been adduced to prove the original and permanent distinctness of species is, that *varieties* produced in a state of domesticity are more or less unstable, and often have a tendency, if left to themselves, to return to the normal form of the parent species; and this instability is considered to be a distinctive peculiarity of all varieties, even of those occurring among wild animals in a state of nature, and to constitute a provision for preserving unchanged the originally created distinct species.

In the absence of scarcity of[3] facts and observations as to *varieties* occurring among wild animals, this argument has had great weight with naturalists, and has led to a very general and somewhat prejudiced belief in the stability of species. Equally general, however, is the belief in what are called "permanent or true varieties,"—races of animals which continually propagate their like, but which differ so slightly (although constantly) from some other race, that the one is considered to be a *variety* of the other. Which is the *variety* and which the original *species*, there is generally no means of determining, except in those rare cases in which the one race has been known to produce an offspring unlike itself and resembling the other. This, however, would seem quite incompatible with the "permanent invariability of species," but the difficulty is overcome by assuming that such varieties have strict limits, and can never again vary further from the original type, although they may return to it, which, from the analogy of the domesticated animals, is considered to be highly probably, if not certainly proved.

It will be observed that this argument rests entirely on the assumption, that *varieties* occurring in a state of nature are in all respects analogous to or even identical with those of domestic animals, and are governed by the same laws as regards their permanence or further variation. But it is the object of the present paper to show that this assumption is altogether false, that there is a general principle in nature which will cause many *varieties* to survive the parent species, and to give rise to successive variations departing further and further from the original type, and which also produces in domesticated animals, the tendency of varieties to return to the parent form.

The Struggle for Existence

The life of wild animals is a struggle for existence. The full exertion of all their faculties and all their energies is required to preserve their own existence and provide for that of their infant offspring. The possibility of procuring food during the least favourable seasons, and of escaping the attacks of their most dangerous enemies, are the primary conditions which determine the existence both of individuals and of entire species. These conditions will also determine the population of

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[3] *Surely Wallace meant to cross out either "absence of" or "scarcity of."*

a species; and by a careful consideration of all the circumstances we may be enabled to comprehend, and in some degree to explain, what at first sight appears so inexplicable—the excessive abundance of some species, while others closely allied to them are very rare.

The Law of Population of Species

The general proportion that must obtain between certain groups of animals is readily seen. Large animals cannot be so abundant as small ones; the carnivora must be less numerous than the herbivora; eagles and lions can never be so plentiful as pigeons and antelopes; the wild asses of the Tartarian deserts cannot equal in numbers the horses of the more luxuriant prairies and pampas of America. The greater or less fecundity of an animal is often considered to be one of the chief causes of its abundance or scarcity; but a consideration of the facts will show us that it really has little or nothing to do with the matter. Even the least prolific of animals would increase rapidly if unchecked, whereas it is evident that the animal population of the globe must be stationary, or perhaps, through the influence of man, decreasing. Fluctuations there may be; but permanent increase, except in restricted localities, is almost impossible. For example, our own observation must convince us that birds do not go on increasing every year in a geometrical ratio, as they would do, were there not some powerful check to their natural increase. Very few birds produce less than two young ones each year, while many have six, eight, or ten; four will certainly be below the average; and if we suppose that each pair produce young only four times in their life, that will also be below the average, supposing them not to die either by violence or want of food. Yet at this rate how tremendous would be the increase in a few years from a single pair! A simple calculation will show that in fifteen years each pair of birds would have increased to nearly ten millions! whereas we have no reason to believe that the number of the birds of any country increases at all in fifteen or in one hundred and fifty years. With such powers of increase the population must have reached its limits, and have become stationary, in a very few years after the origin of each species. It is evident, therefore, that each year an immense number of birds must perish—as many in fact as are born; and as on the lowest calculation the progeny are each year twice as numerous as their parents, it follows that, whatever be the

average number of individuals existing in any given country, *twice that number must perish annually*,—a striking result, but one which seems at least highly probable, and is perhaps under rather than over the truth. It would therefore appear that, as far as the continuance of the species and the keeping up the average number of individuals are concerned, large broods are superfluous. On the average all above *one* become food for hawks and kites, wild cats and weasels, or perish of cold and hunger as winter comes on. This is strikingly proved by the case of particular species; for we find that their abundance in individuals bears no relation whatever to their fertility in producing offspring. Perhaps the most remarkable instance of an immense bird population is that of the passenger pigeon of the United States, which lays only one, or at most two eggs, and is said to rear generally but one young one. Why is this bird so extraordinarily abundant, while others producing two or three times as many young are much less plentiful? The explanation is not difficult. The food most congenial to this species, and on which it thrives best, is abundantly distributed over a very extensive region, offering such difference of soil and climate, that in one part or another of the area the supply never fails. The bird is capable of a very rapid and long-continued flight, so that it can pass without fatigue over the whole of the district it inhabits, and as soon as the supply of food begins to fail in one place is able to discover a fresh feeding-ground.[4] This example strikingly shows us that the procuring a constant supply of wholesome food is almost the sole condition requisite for ensuring the rapid increase of a given species, since neither the limited fecundity, nor the unrestrained attacks of birds of prey and of man are here sufficient to check it. In no other birds are these peculiar circumstances so strikingly combined. Either their food is more liable to failure, or they have not sufficient power of wing to search for it over an extensive area, or during some season of the year it becomes very scarce, and less wholesome substitutes have to be found; and thus, though more fertile in offspring, they can never increase be-

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[4] *Wallace's account offers an insight into what happened to the passenger pigeon. It became extinct early in the twentieth century, in part because of extensive hunting, but also because of the widespread loss of habitat to a settled, modern human population and because, as Wallace notes, it was not very good at reproducing itself, even when, very late in the game, people began to say that something should be done to ensure the bird's survival.*

yond the supply of food in the least favourable seasons. Many birds can only exist by migrating, when their food becomes scarce, to regions possessing a milder, or at least a different climate, though, as these migrating birds are seldom excessively abundant, it is evident that the countries they visit are still deficient in a constant and abundant supply of wholesome food. Those whose organization does not permit them to migrate when their food becomes periodically scarce, can never attain a large population. This is probably the reason why woodpeckers are scarce with us, while in the tropics they are among the most abundant of solitary birds. Thus, the house sparrow is more abundant than the redbreast, because its food is more constant and plentiful,—seeds of grasses being preserved during the winter, and our farm-yards and stubble-fields furnishing an almost inexhaustible supply. Why, as a general rule, are aquatic, and especially sea birds, very numerous in individuals? Not because they are more prolific than others, generally the contrary; but because their food never fails, the sea-shores and river-banks daily swarming with a fresh supply of small mollusca and crustacea. Exactly the same laws will apply to mammals. Wild cats are prolific and have few enemies; why then are they never as abundant as rabbits? The only intelligible answer is, that their supply of food is more precarious. It appears evident, therefore, that so long as a country remains physically unchanged, the numbers of its animal population cannot materially increase. If one species does so, some other requiring the same kind of food much diminish in proportion. The numbers that die annually must be immense; and as the individual existence of each animal depends upon itself, those that die must be the weakest—the very young, the aged, and the diseased,—while those that prolong their existence can only be the most perfect in health and vigour—those who are best able to obtain food regularly, and avoid their numerous enemies. It is, as we commenced by remarking, "a struggle for existence," in which the weakest and least perfectly organized must always succumb.

The Abundance or Rarity of a Species Dependent Upon Its More or Less Perfect Adaptation to the Conditions of Existence

It seems evident that what takes place among the individuals of a species must also occur among the several allied species of a group,—viz., that those which are best adapted to obtain a regular supply of

food, and to defend themselves against the attacks of their enemies and the vicissitudes of the seasons, must necessarily obtain and preserve a superiority in population; while those species which from some defect of power or organization are the least capable of counteracting the vicissitudes of food, supply, &c., must diminish in numbers, and, in extreme cases, become altogether extinct. Between these extremes the species will present various degrees of capacity for ensuring the means of preserving life; and it is thus we account for the abundance or rarity of species. Our ignorance will generally prevent us from accurately tracing the effects to their causes; but could we become perfectly acquainted with the organization and habits of the various species of animals, and could we measure the capacity of each for performing the different acts necessary to its safety and existence under all the varying circumstances by which it is surrounded, we might be able even to calculate the proportionate abundance of individuals which is the necessary result.

If now we have succeeded in establishing these two points—1st, *that the animal population of a country is generally stationary, being kept down by a periodical deficiency of food, and other checks*; and, 2nd, *that the comparative abundance or scarcity of the individuals of the several species is entirely due to their organization and resulting habits, which, rendering it more difficult to procure a regular supply of food and to provide for their personal safety in some cases than in others, can only be balanced by a difference in the population which have to exist in a given area*—we shall be in a condition to proceed to the consideration of *varieties*, to which the preceding remarks have a direct and very important application.

Useful Variations Will Tend to Increase; Useless or Hurtful Variations to Diminish

Most or perhaps all the variations from the typical form of a species must have some definite effect, however slight, on the habits or capacities of the individuals. Even a change of colour might, by rendering them more or less distinguishable, affect their safety; a greater or less development of hair might modify their habits. More important changes, such as an increase in the power or dimensions of the limbs or any of the external organs, would more or less affect their mode of procuring food or the range of country which they inhabit. It is also

evident that most changes would affect, either favourably or adversely, the powers of prolonging existence. An antelope with shorter or weaker legs must necessarily suffer more from the attacks of the feline carnivora; the passenger pigeon with less powerful wings would sooner or later be affected in its powers of procuring a regular supply of food; and in both cases the result must necessarily be a diminution of the population of the modified species. If, on the other hand, any species should produce a variety having slightly increased powers of preserving existence, that variety must inevitably in time acquire a superiority in numbers. These results must follow as surely as old age, intemperance, or scarcity of food produce an increased mortality. In both cases there may be many individual exceptions; but on the average the rule will invariably be found to hold good. All varieties will therefore fall into two classes—those which under the same conditions would never reach the population of the parent species, and those which would in time obtain and keep a numerical superiority. Now, let some alteration of physical conditions occur in the district—a long period of drought, a destruction of vegetation by locusts, the irruption of some new carnivorous animal seeking "pastures new"—any change in fact tending to render existence more difficult to the species in question, and tasking its utmost powers to avoid complete extermination; it is evident that, of all the individuals composing the species, those forming the least numerous and most feebly organized variety would suffer first, and, were the pressure severe, must soon become extinct. The same causes continuing in action, the parent species would next suffer, would gradually diminish in numbers, and with a recurrence of similar unfavourable conditions might also become extinct. The superior variety would then alone remain, and on a return to favourable circumstances would rapidly increase in numbers and occupy the place of the extinct species and variety.

Superior Varieties Will Ultimately Extirpate the Original Species

The *variety* would now have replaced the *species*, of which it would be a more perfectly developed and more highly organized form. It would be in all respects better adapted to secure its safety, and to prolong its individual existence and that of the race. Such a variety *could not* return to the original form; for that form is an inferior one, and could never compete with it for existence. Granted, therefore, a

"tendency" to reproduce the original type of the species, still the variety must ever remain preponderant in numbers, and under adverse physical conditions *again alone survive*. But this new, improved, and populous race might itself, in course of time, give rise to new varieties, exhibiting several diverging modifications of form, any of which, tending to increase the facilities for preserving existence, must by the same general law, in their turn become predominant. Here, then, we have *progression and continued divergence* deduced from the general laws which regulate the existence of animals in a state of nature, and from the undisputed fact that varieties do frequently occur. It is not, however, contended that this result would be invariable; a change of physical conditions in the district might at times materially modify it, rendering the race which had been the most capable of supporting existence under the former conditions now the least so, and even causing the extinction of the newer and, for a time, superior race, while the old or parent species and its first inferior varieties continued to flourish. Variations in unimportant parts might also occur, having no perceptible effect on the life-preserving powers; and the varieties so furnished might run a course parallel with the parent species, either giving rise to further variations or returning to the former type. All we argue for is, that certain varieties have a tendency to maintain their existence longer than the original species, and this tendency must make itself felt; for though the doctrine of chances or averages can never be trusted to on a limited scale, yet, if applied to high numbers, the results come nearer to what theory demands, and, as we approach to an infinity of examples, become strictly accurate. Now the scale on which nature works is so vast—the numbers of individuals and periods of time with which she deals approach so near to infinity, that any cause, however slight, and however liable to be veiled and counteracted by accidental circumstances, must in the end produce its full legitimate results.

The Partial Reversion of Domesticated Varieties Explained

Let us now turn to domesticated animals, and inquire how varieties produced among them are affected by the principles here enunciated. The essential difference in the condition of wild and domestic animals is this,—that among the former, their well-being and very existence depend upon the full exercise and healthy condition of all their senses

and physical powers, whereas, among the latter, these are only partially exercised, and in some cases are absolutely unused. A wild animal has to search, and often to labour, for every mouthful of food—to exercise sight, hearing, and smell in seeking it, and in avoiding dangers, in procuring shelter from the inclemency of the seasons, and in providing for the subsistence and safety of its offspring. There is no muscle of its body that is not called into daily and hourly activity; there is no sense or faculty that is not strengthened by continual exercise. The domestic animal, on the other hand, has food provided for it, is sheltered, and often confined, to guard it against the vicissitudes of the seasons, is carefully secured from the attacks of its natural enemies, and seldom even rears its young without human assistance. Half of its senses and faculties are quite useless; and the other half are but occasionally called into feeble exercise, while even its muscular system is only irregularly called into action.

Now when a variety of such an animal occurs, having increased power or capacity in any organ or sense, such increase is totally useless, is never called into action, and may even exist without the animal ever becoming aware of it. In the wild animal, on the contrary, all its faculties and powers being brought into full action for the necessities of existence, any increase becomes immediately available, is strengthened by exercise, and must even slightly modify the food, the habits, and the whole economy of the race. It creates as it were a new animal, one of superior powers, and which will necessarily increase in numbers and outlive those inferior to it.

Again, in the domesticated animal all variations have an equal chance of continuance; and those which would decidedly render a wild animal unable to compete with its fellows and continue its existence are no disadvantage whatever in a state of domesticity. Our quickly fattening pigs, short-legged sheep, pouter pigeons, and poodle dogs could never have come into existence in a state of nature, because the very first step towards such inferior forms would have led to the rapid extinction of the race; still less could they now exist in competition with their wild allies. The great speed but slight endurance of the race horse, the unwielding strength of the ploughman's team, would both be useless in a state of nature. If turned wild on the pampas, such animals would probably soon become extinct, or under favorable circumstances might each lose those extreme qualities which would

never be called into action, and in a few generations would revert to a common type, which must be that in which the various powers and faculties are so proportioned to each other as to be best adapted to procure food and secure safety,—that in which by the full exercise of every part of his organization the animal can alone continue to live. Domestic varieties, when turned wild, *must* return to something near the type of the original wild stock, *or become altogether extinct.*

Lamarck's Hypothesis Very Different from That Now Advanced

We see, then, that no inference as to varieties in a state of nature can be deduced from the observation of those occurring among domestic animals. The two are so much opposed to each other in every circumstance of their existence, that what applies to the one is almost sure not to apply to the other. Domestic animals are abnormal, irregular, artificial; they are subject to varieties which never occur and never can occur in a state of nature; their very existence depends altogether on human care: so far are many of them removed from that just proportion of faculties, that true balance of organization, by means of which alone an animal left to its own resources can preserve its existence and continue its race.

The hypothesis of Lamarck—that progressive changes in species have been produced by attempts of animals to increase the development of their own organs, and thus modify their structure and habits—has been repeatedly and easily refuted by all writers on the subject of varieties and species, and it seems to have been considered that when this was done the whole question has been finally settled; but the view here developed renders such an hypothesis quite unnecessary, by showing that similar results must be produced by the action of principles constantly at work in nature. The powerful retractile talons of the falcon- and the cat-tribes have not been produced or increased by the volition of those animals; but among the different varieties which occurred in the earlier and less highly organized forms of these groups, *those always survived longest which had the greatest facilities for seizing their prey.* Neither did the giraffe acquire its long neck by desiring to reach the foliage of the more lofty shrubs, and constantly stretching its neck for the purpose, but because any varieties which occurred among its antitypes with a longer neck than usual *at once secured a fresh range of pasture over the same ground*

as their shorter-necked companions, and on the first scarcity of food were thereby enabled to outlive them. Even the peculiar colours of many animals, especially insects, so closely resembling the soil or the leaves or the trunks on which they habitually reside, are explained on the same principle; for though in the course of ages varieties of many tints have occurred, *yet those races having colours best adapted to concealment from their enemies would inevitably survive the longest.* We have also here an acting cause to account for that balance so often observed in nature,—a deficiency in one set of organs always being compensated by an increased development of some others—powerful wings accompanying weak feet, or great velocity making up for the absence of defensive weapons; for it has been shown that all varieties in which an unbalanced deficiency occurred could not long continue their existence. The action of this principle is exactly like that of the centrifugal governor of the steam engine, which checks and corrects any irregularities almost before they become evident; and in like manner no unbalanced deficiency in the animal kingdom can ever reach any conspicuous magnitude, because it would make itself felt at the very first step, by rendering existence difficult and extinction almost sure to follow. An origin such as is here advocated will also agree with the peculiar character of the modifications of form and structure which obtain in organized beings—the many lines of divergence from a central type, the increasing efficiency and power of a particular organ through a succession of allied species, and the remarkable persistence of unimportant parts such as colour, texture of plumage and hair, forms of horns or crests, through a series of species differing considerably in more essential characters. It also furnishes us with a reason for that "more specialized structure" which Professor Owen states to be a characteristic of recent compared with extinct forms, and which would evidently be the result of the progressive modification of any organ applied to a special purpose in the animal economy.

Part III

Beyond The Origin
The Nature of Inheritance

Introduction

Eiseley, Loren: *Darwin's Century: The Priest Who Held the Key to Evolution*, Chapter 8

Beyond *The Origin* – The Nature of Inheritance: Introduction

Scientific progress is often thought of as a series of replacements. A theory with greater power to explain natural phenomena replaces one that is less able to provide complete and satisfying answers to our questions. A superior theory, once it is considered and tested by scientists (and other interested people), naturally will become the established way of thinking about nature. That's what we're told, after all.

The fact that the greatest, and simplest, theory about how heredity works was ignored by the best minds of the day, for the greater part of fifty years, is therefore quite troubling. You can look at the life and work of Gregor Mendel as a series of professional disappointments and bad luck; however, you can also see the eventual triumph of his thinking as a vindication of how scientific progress is supposed to work. The better theory did win out in the end; it just took time to be recognized for the work of genius that it is.

This essay, by Professor of Anthropology Loren Eiseley, is about the enormous change in scientific thinking that was necessary before Mendel's mathematically elegant ideas about heredity could be accepted. In many ways, this change is similar to the shift in human understanding that preceded the acceptance of Copernicus', Galileo's, and Kepler's ideas about the architecture of the universe, and Newton's explanations of planetary motion. Thomas Kuhn termed this kind of great change in ways of thinking about nature a paradigm shift. We tend to think of Newton as a solitary genius, but his contribution was built upon the work of earlier physicists, a fact Newton himself acknowledged. Similarly, Mendel's work was based in the groundbreaking analysis of biological evolution that was the lifework of Charles Darwin and Alfred Russel Wallace. Mendel knew Darwin's work well. Darwin, if he ever heard of Mendel, did not see in the patient work of this German monk the answer to the most tantalizing question posed by evolutionary theories: how does variation enter a population, and how is it transmitted to succeeding generations? Mendel, as Eiseley points out, actually solved this central problem by looking at the opposite question: how do traits persist in a population, and how are they transmitted faithfully to offspring?

Mendel's work was largely ignored after its publication, and he did not receive the recognition for answering the central problem of evolution until long after his death. Eiseley points out, however, that this long delay can be attributed to several factors. First, no one, in the late nineteenth century, knew how germ cells differed from somatic cells, or even if Mendel's "allele" (the form of a trait) could be present in cellular structures. Second, observation of the genetics of domestic plants and animals had led many scientists (Darwin, included) to consider that heredity worked by blending the traits of the parents in the offspring. Darwin's tortuous explanation of blending inheritance was largely a response to criticism of his evolutionary theory by Scottish engineer Fleeming Jenkin, and was not a satisfying explanation of how variation could enter a population. The work of August Weismann laid the foundation of cellular genetics, and the understanding that cellular structures could hold and transmit genetic information. Similarly, the work of W.L. Johannsen showed that genetic change was limited in a species, and that there was a direct correlation between the genotype (the cellular determinant of heredity) and the phenotype (the outward appearance) of an individual. The work of Galileo and Kepler changed Copernicus' explanation of the solar system from heretical to inevitable. Similarly, Weismann and Johannsen showed that Mendel's elegant theory held the key to understanding the mechanisms of biological evolution.

Questions to consider:

1. Why is persistence of a trait, rather than introduction of variation, important in understanding hereditary transmission?

2. What was Fleeming Jenkin's challenge to Darwin? Why did Darwin take this challenge so seriously?

3. How does Darwin's idea of 'gemmules' compare with Weismann's idea of a germ plasm? Why is Weismann's idea more convincing?

4. How does the word 'mutation' apply to Johannsen's work? What does mutation mean in Hugo de Vries' work?

SKSS

Chapter VIII

The Priest Who Held the Key to Evolution

> Great revolutions in science are scarcely ever effected but after their authors have ceased to breathe.
>
> *William Swainson*, 1834

I *Gregor Mendel*

"On a clear, cold evening in February," so his biographer states, for the record is clearer upon the weather of this particular evening of 1865 than upon the momentous event that occurred in it, "Father Gregor Mendel read before the Brünn Society for the Study of Natural Science, his paper upon 'Experiments in Plant Hybridization.'"[1] Forty people were present in the room at the schoolhouse where the lecture was given. They were not ignorant people. Botanists, a chemist, an astronomer, a geologist were among those present. In the next month Mendel spoke again to the same audience recounting before them his new theory upon the nature of inheritance. The audience listened patiently. At the end of the blue-eyed priest's eager presentation of his researches, the still

[1] Hugo Iltis, *Life of Mendel*, New York, 1932.

existing minutes of the society indicate there was no discussion.

Stolidly the audience had listened. Just as stolidly it had risen and dispersed down the cold, moonlit streets of Brünn. No one had ventured a question, not a single heartbeat had quickened. In the little schoolroom one of the greatest scientific discoveries of the nineteenth century had just been enunciated by a professional teacher with an elaborate array of evidence. Not a solitary soul had understood him.

Thirty-five years were to flow by and the grass on the discoverer's grave would be green before the world of science comprehended that tremendous moment. Aged survivors from the little audience would then be importuned for their memories. Few would have any.

In the four huge volumes in which, at the end of the century, the scientific historian John Merz records a hundred years of discovery, the name Gregor Mendel receives only footnote mention. Yet with Lamarck and Charles Darwin he shares today the biological honors of the nineteenth century. It is *par excellence* the century that discovered time and change. Perhaps as a consequence there is something a little symbolic about the lives of these three men. Lamarck died in forgotten poverty, but above his grave rang his daughter's defiant outcry, "The future will remember you, my father." Charles Darwin had been more fortunate in the world's adulation, yet a decade after the publication of the *Origin* he was to hesitate and fall back upon a theory which weakened his life's work and which would have proved unnecessary had he known what was said on that winter evening of 1865 in Brünn.

Darwinism, after the rediscovery of Mendel, was to undergo a sea change. It was to be half dismissed by Mendel's first followers and then emerge once more strengthened, enriched, and rejuvenated by the discoveries which flowed from the work of the obscure priest who read the

Origin of Species and carried on queer experiments with peas which he affectionately referred to as his children. From peas, dwarfed, wrinkled, yellow, tall, short, he was to derive the laws which make modern genetics one of the most exact of the biological sciences. He had probed into the mysteries of the cell without a microscope. He had done it by infinite patience alone in the solitude of a monastery garden.

Although his observations were reported to the world, they lay unread. "My time will come," he said once to his friend Niessl, but it is doubtful if by then he really believed it. When he died in 1884, it was as a prelate of the church, worn out with the cares of office. His experiments had long since ceased. They had never aroused public attention and perhaps in the end, alone, confused, and ill-advised by the only botanist he knew, he had come to doubt their value. A few years after his election as prelate a visitor wishing to observe the experimental plants at the monastery reported simply, "I found that I had come too late." In a similar way fame came at last to Gregor Mendel.

There is perhaps no stranger story in the annals of science than the rise to international eminence of this solitary man sixteen years after his death and thirty-five years after the talk in the little hall at Brünn. It is a story which is worth perusal by all scholars, not alone because of what Mendel achieved, but also because the complete failure of communication in this particular instance was, to a major degree, the failure of professional science. It has its lessons, even though the world has changed greatly since 1865. No man who loves knowledge would want an episode like this to happen twice.

Some scientists have tried to argue that the journal in which Mendel published was obscure, but his tragedy is more profound than this. He was advised by one of the great European botanists of his generation and he was betrayed, not consciously, we may say in charity, but be-

trayed through condescension. Mendel was an amateur and the professional scientist whom he looked up to and admired saw in him no more than an instrument for the furtherance of his own researches. It is true that the intellectual climate of the time increased his difficulties, but it is also true that Mendel, this man of buoyant good will, was denied throughout his life the solace of a single sincere professional friend who would lend an understanding ear to the account of his experiments.

From first to last Mendel was dogged by ill luck in everything that mattered save just one thing: the choice of the edible pea for his experiments. Even this plant, with its luckily simple genetic structure, was eventually abandoned—once more by professional scientific advice. Indeed, at this late point in time one might readily wonder how much he really glimpsed of the significance of his own discoveries—one might, that is, if one did not know of the well-stocked monastery library with its annotated copy of Darwin. We know, too, that he tried experiments to test the Lamarckian principle. Alone in his garden he had wrestled with the two leading theories involving organic evolution, but where Darwin and Lamarck had been fascinated by change, Mendel was fascinated by stability. Instead of attempting, as did Darwin, to determine how the characteristics of the adult organism were transferred to, or compressed into, a minute germ cell, Mendel sought to determine how it came about that the germ cell contained and transmitted the characters of the living animal.

Mendel, in other words, had intuitively grasped what seemingly no one else of his generation understood; namely, that until we had some idea of the mechanisms which controlled organic *persistence* we would be ill-equipped to understand what it was that produced evolutionary change. The persistence of biological form in time is the first fact in our experience. Organic change is a far more subtle phenomenon whose detection, as we have

had occasion to observe, is dependent upon a sophisticated knowledge of successive plant and animal transformations occurring throughout great stretches of the past. It is for this reason that evolution remained so long undetected, whereas the assumption of special creation of each species struck very few as being in the least illogical.

It was Mendel's virtue that he concentrated with more precision than anyone before him upon the way in which already existing characters emerged or failed to emerge in the offspring of a particular union. In examining the details of his unfortunate career it will be possible to see with greater clarity why Darwin by 1871 in the *Descent of Man* was expressly retreating from his bold stand upon natural selection as the major factor in the production of evolutionary change. In that volume Darwin, quite in contrast with his assurance of 1859, wrote as follows: "I now admit . . . that in the earlier editions of my 'Origin of Species' I perhaps attributed too much to the action of natural selection or the survival of the fittest."[2]

There was a reason for this wary retreat on the part of the master. Ironically enough, two years after Mendel had actually placed a possible answer to Darwin's problem on record, a very erudite Scotch engineer brought forward in the pages of the *North British Review*[3] a formidable challenge to the Darwinians. It was a challenge which only a Mendelian geneticist could have answered—and Mendel, immured in his monastery, was unknown to both parties.

Darwin never attempted a direct response to Jenkin—he always avoided public controversy—but there is ample testimony in his letters to the effect which Jenkin's criticism had upon him. "Fleeming Jenkin has given me much trouble . . ." he wrote to Hooker in January of 1869.[4] In

[2] C. Darwin, *Descent of Man*, 1871, Modern Library ed., p. 441.
[3] Fleeming Jenkin, "The Origin of Species," *North British Review*, 1867, Vol. 46, pp. 149–71.
[4] LLD, Vol. 2, p. 379.

February he confided to Wallace: "Jenkin argued in the 'North British Review' against single variations ever being perpetuated, and has convinced me. . . ." Finally, in the sixth edition of the *Origin of Species* one may read his open confession: "Nevertheless, until reading an able and valuable article in the 'North British Review' (1867) I did not appreciate how rarely single variations, whether slight or strongly marked, could be perpetuated. . . . The justice of these remarks cannot, I think, be disputed."[5]

The reader must now consider what is implied in the above statements. Fleeming Jenkin had, in actuality, well-nigh destroyed the fortuitous character of variation as it was originally visualized by Darwin. Jenkin set forth the fact that a newly emergent character possessed by one or a few rare mutants would be rapidly swamped out of existence by backcrossing with the mass of individuals that did not possess the trait in question. Only if the same trait emerged *simultaneously* throughout the majority of the species could it be expected to survive.

An admission that numbers of animals or plants mutate simultaneously in the same direction, however, greatly reduces the significance of natural selection and suggests either some interior orthogenetic drive which is affecting the individual members of the species, or an external environmental force of Lamarckian character producing a direct effect on the germ plasm of an entire group of organisms. In either case fluctuating fortuitous individual variation has to be abandoned and with it goes much of the importance of natural selection.[6] Jenkin's formidable mathematical attack, formidable, that is, in the light of the conception of blending inheritance prevalent at the time, seemed to Darwin largely unanswerable. The only recourse was to fall back toward the type of Lamarckian-

[5] Modern Library ed., p. 71.

[6] J. C. Willis, *The Course of Evolution*, Cambridge University Press, 1940, pp. 5, 165–66. Also H. J. Muller, "The Views of Haeckel in the Light of Genetics," *Philosophy of Science*, 1934, Vol. 1, p. 318.

ism around which he elaborated his theory of pangenesis. Darwin died with this difficulty unsolved and its consequences haunting his last years. The answer to Fleeming Jenkin had been standing on library shelves in the Proceedings of the Brünn Society for the Study of Natural Science since 1866. Jenkin, the hardheaded engineer, and the gracious, dreaming naturalist who had been forced to retreat before him would both be gone before anyone blew the dust from those forgotten pages.

Mendel is a curious wraith in history. His associates, his followers, are all in the next century. That is when his influence began. Yet if we are to understand him and the way in which he eventually rescued Darwinism itself from oblivion we must go the long way back to Brünn in Moravia and stand among the green peas in a quiet garden. Gregor Mendel had a strange fate: he was destined to live one life painfully in the flesh at Brünn and another, the intellectual life of which he dreamed, in the following century. His words, his calculations were to take a sudden belated flight out of the dark tomblike volumes and be written on hundreds of university blackboards, and go spinning through innumerable heads. Before their importance can be grasped, however, it is necessary to examine the state of genetics at the time Darwin wrote the *Origin of Species* and to gain some idea of the nature of the menace which confronted Darwin upon the publication of Jenkin's paper.[7]

II Pre-Mendelian Genetics

The earlier history of human genetics is an amazing assemblage of superstitious error and fallacious observation. Monstrous births were assumed to be the result of man-animal connections. Right down into the eighteenth century such reports continued to be printed. As I remarked

[7] It can also be found in his *Papers, Literary, Scientific, Etc.*, ed. by Sidney Colvin and J. A. Ewing, London, 1887, Vol. 1.

on an earlier page, the fixed precision of Christian speciation really represents in no small degree a late amalgamation of Linnaean scientific taxonomy with the increasing Christian emphasis upon special creation.[8] Monstrous hybrids between men, bears, and other animals which no educated person would accept today were taken quite seriously right into De Maillet's time—an added reason, incidentally, for not dismissing as romantics, or as unscientific, scholars who were merely repeating the common beliefs of their day.[9] Undoubtedly some of the floating beliefs that plants could change their type—ideas which survive in the pages of the *Vestiges*—were derived from accidental cases of genuine plant hybridity and mutation. Anecdote and tall tale were the common data of genetics until well into the latter part of the eighteenth century. At that time the rise of professional breeding and the growing interest in the importation of valuable food and drug plants began to place emphasis upon controlled experimentation. The idea of selective livestock breeding arose in England during the early phases of the Industrial Revolution when the multiplying towns began to demand meat and dairy produce on a large scale. What emerged, and stimulated practical improvement in livestock, was the shift from purely local subsistence farming to the profitable business of supplying the food and wool needs of the new industrial towns. All of these purely economic factors greatly stimulated experimentation among commercial breeders. Darwin, who had come from the country, early showed a shrewd instinct for merging the theoretical with the practical when he began his intensive perusal of horticultural and livestock journals.

If we are to get clearly in mind the difference between the genetics of Darwin's day and the sort of problems

[8] E. B. Poulton in *Essays on Evolution*, Oxford, 1908, p. 56, suggests seventeenth-century Puritan influence.

[9] Conway Zirkle in *The Beginnings of Plant Hybridization*, Philadelphia, 1935, gives an extended historical account of fantastic animal combinations.

which began to emerge toward the close of the century we must remember that all the great cytological work upon cell mechanisms was unavailable to both Darwin and Mendel. Their observations were confined to direct breeding experiments, or what they could learn from others. Mendel, as we have intimated, approached the problem in a quite different way from Darwin and proved to be the better experimentalist. Perhaps he was fortunate, so far as his experiments went, in not being a famous man already laboring under a point of view.

We have already learned the general nature of Darwin's beliefs. Here we are concerned only with the contrast he was later to make with Wallace on the one hand and, later on and posthumously, with the Mendelians on the other. Just as in the case of Darwin's evolutionary thinking, it is not always easy to isolate, out of the vast mass of his accumulated examples, the precise outlines of his genetic ideas. It is very commonly stated that Darwin believed in blending inheritance, while Mendel succeeded in demonstrating the reality of particulate inheritance. This appears to me a mild oversimplification of a more complicated situation. The confusion is emphasized when one comes to remark that Romanes, in discussing Darwin's views a few years prior to the rediscovery of Mendel, classifies Darwin's theory of heredity as a particulate one.[10]

Actually it would seem that the case might be better put as follows. Prior to the emergence of the critiques of A. W. Bennett and Fleeming Jenkin it would appear that Darwin had taken a great deal of the genetics of his day for granted. His primary interest, because of his evolutionary studies, lay in the field of variation. In the first edition of the *Origin* he simply states that the laws governing in-

[10] G. J. Romanes, *Darwin and after Darwin*, Chicago, 1897, Vol. 2, p. 45. E. S. Russell in *The Interpretation of Development and Heredity*, Oxford, 1930, p. 63, similarly expresses himself and cites Johannsen to the same effect.

heritance are quite unknown, though he is vaguely aware of phenomena that today would go under such categories as sex-linked inheritance, or dominance and recessiveness. He confesses that variability is governed by unknown laws, but he realizes that this variability is without significance unless its benefits can be retained and accumulated through heredity. Drawing upon the forceful analogy of domestic breeding he professes to see no limit to the transmuting power of nature.

As one studies this first edition of the *Origin* one can see that in spite of the author's enthusiasm for natural selection he is rather careful to mention all factors which could conceivably play a part in organic change. As we have remarked, he remains, in this sense, a transitional figure. His genetics is essentially that of the shrewd out-of-doors observer. He is neither particulate in any precise sense, nor does he incline totally toward blending conceptions of inheritance. In reality he is occupied with just two things: variation and natural selection. He is thinking about evolution and his views have not yet been proved vulnerable by means of heredity. It was the attack launched by Jenkin and Bennett that forced Darwin into a more elaborate treatment of genetic mechanisms and led eventually to a retreat down one of the pathways he had left open for himself. The retreat was not dictated through Jenkin's criticism alone. His troubles were augmented by events in the field of geophysics which we will chronicle in the next chapter.

When Jenkin penned his attack on natural selection it is quite obvious that he had found a loophole which Darwin, who was not mathematically gifted, had entirely overlooked. In brief, Jenkin simply took the position:

1. That it was not possible in domestic breeding to push a strain beyond a certain point of maximum efficiency for a given character. In his analysis of this problem Jenkin appears to have theoretically anticipated the later discoveries of Johannsen in the field of fluctuating variation.

In this, however, he was ahead of his time and the debates which would later emerge around that subject. The attack which really shook Darwin was:

2. The argument that a favorable mutative sport would be "utterly outbalanced by numerical inferiority." Since the unblending character of Mendelian units was unknown, Jenkin's position was simply that a single favorable mutation would soon be swamped out and by degrees obliterated in any population group in which it occurred. Since the favored animal or plant would presumably be mating with its normal fellows, the rare variation would not long survive. As a potent example Jenkin advanced the hypothetical case of a single well-endowed white man being cast ashore on an island inhabited by Negroes. No matter how much power he might attain among them, the tribe would certainly not become white because of his presence. The only answer, ignoring for the moment Mendelian genetics, is to postulate a large group of animals mutating in a similar direction and contemporaneously. Jenkin points out this alternative, though, as he justly observes, it results in an evolution which is no longer the product of chance and selection but rather "a theory of successive creations." The fortuitous element involved in natural selection disappears and one is immediately confronted, not with accident, but an orthogenetic and controlled movement in a single direction. Darwin was sufficiently impressed by this argument that, although he did not abandon his book, he incorporated into it the Jenkin alternative suggestion and began at the same time a retreat toward habit and use-inheritance which it is obvious he now saw as a refuge from the corner into which he had been forced by Jenkin. A. W. Bennett pressed the same advantage in another paper three years later in *Nature*[11] and Herbert Spencer, one of England's pre-

[11] "The Theory of Selection from a Mathematical Point of View," *Nature*, 1870, Vol. 3, pp. 30–31.

Darwinian evolutionists, reiterated the Jenkin position as late as 1893.[12]

The final edition of the *Origin* contains, in the light of Jenkin's views, some quite surprising comment. "There must be some efficient cause for each slight individual difference," Darwin says, "as well as for more strongly marked variations which occasionally arise; and if the unknown cause were to act persistently, *it is almost certain that all the individuals of the species would be similarly modified.*"[13] (Italics mine. L.E.) In those lines Darwin has assumed the Jenkin argument which permits the retention of evolution but at the price of fortuitous variation. One line further, however, and we encounter the contention that he has underrated "the frequency and importance of modifications due to spontaneous variability."

Darwin with his gift for compromise has here accepted both a point of view which, if pursued, would be metaphysically fatal to his system and, at the same time, has stepped up the pace of variation to try to overcome the logic of Jenkin's argument. The number of these concealed contradictions makes the later editions of the *Origin* instructive but difficult reading. For clarity and reasonable consistency the first edition is by far the most satisfactory.

III Pangenesis

In 1868 Darwin published the *Variation of Animals and Plants under Domestication.* In it, for the first time, he set forth a theory of inheritance to which he applied the term "pangenesis." This theory actually implies a type of particulate inheritance, although Darwin's concern over Jenkin's paper quite obviously reveals that this assumption of blending inheritance raised no question in his

[12] "The Inadequacy of Natural Selection," *Popular Science Monthly*, 1893, Vol. 42, p. 807.
[13] Modern Library ed., p. 155–56.

mind in 1867. Pangenesis, however, is a theory of particulate inheritance beginning at the other end, so to speak, of the problem Mendel pursued. It begins, that is, with the assemblage of another potential individual from the body cells of an existing organism. It is not an idea originating with Darwin by any means; it runs all the way back to the Greeks,[14] but Darwin's elaboration of it is an indirect escape from such problems as Bennett and Jenkin had formulated.

Darwin assumed that the cells of the body throw off minute material particles and that these particles, "gemmules," he calls them, are gathered from all parts of the body into the sexual cells of the organism. Darwin thus assumes that the sexual cells contain only what is represented in the living body—or primarily so—and the particles they receive upon fertilization. Every character thus comes from the somatic, or body, tissues, and the germ cells contain only what is brought to them by the blood stream from all parts of the body. The germ is merely a device to create a new body out of the mingling of the particles of the parents' bodies.

Darwin's germ materials are thus developed anew with every living individual. This is in marked contradiction to later theories about the inviolability of the germ plasm. It permits any somatic modification during an individual's lifetime to be represented in his germ cells. It is, in other words, a Lamarckian device ensuring the inheritance of adaptive modifications in unending succession. That Darwin should have proposed this theory indicates, not alone how inadequate natural selection had come to seem to him, but how truly transitional, in retrospect, we can observe his thinking to be. He is half modern, half experimental, yet in times of difficulty he is capable of obscure retreats in the direction of eighteenth-century concepts. August Weismann (1834–1914), the man who reversed the trend of particulate studies, and who has been termed

[14] M. J. Sirks, *General Genetics*, The Hague, 1956, p. 49 ff.

the first original evolutionist after Darwin,[15] has himself remarked that he would probably never have been led to deny the inheritance of acquired characters if it had not been for the impossible complications involved in "the giving off, circulation, and accumulation of gemmules."[16]

In spite of the fact that Weismann remained sufficiently hypnotized by the omnipresent Darwinian shadow to postulate a "struggle" among the determiners in the germ cell, he actually diverted the study of evolution into the pathway which has led on to the great modern advances in the field of genetics. We have seen that Darwin's determiners were supposed to arise in the body cells and to carry, in some mysterious manner, the image of their particular body region compacted into a newly produced germ cell.

Weismann, on the other hand, reversed the attention which had been directed to the body as a source of variation, and concentrated his attention upon the germ itself as the source of emergent change. He postulated a germ plasm which was basically immortal and inviolable. By this he meant that the reproductive cells are isolated early and are passed along unchanged from individual to individual in the history of the race. By "unchanged" is meant unaffected by exterior environmental influences. All changes which emerge in the phylogeny of a given organism must therefore emerge from the alteration or elimination of particular hereditary determiners within the germ plasm itself, not from "messenger" determiners carried into the germ from sources in the adult body. It has been said by many modern writers that Weismann carried this inviolability principle too far, but it should be remarked in simple justice that since his works are no longer read in great detail, his own qualifications upon this point have been forgotten. He was willing to concede that the germ plasm was probably not totally isolable from

[15] Mendel, of course, being unknown.
[16] *Essays upon Heredity*, Oxford, 1892, Vol. 2, pp. 80–81.

influences penetrating it from the body, but that such influences "must be extremely slight."[17] It must be remembered that Weismann was combating Darwin's notion of a great stream of "messengers" entering the germ plasm from the body itself. There is no reason to think that Weismann, if he were alive today, would find it necessary to cavil over mutations produced in the germ plasm by radiation or by other similar powerful forces exerted upon the body.

In summary then, we may say that while it has long since been disproved that the determiners engage in a struggle for existence within the germ cell, the main features of Weismann's system have been retained as the actual basis of modern genetics. Germ cells come from other germ cells and are not derived from body cells. Germinal continuity is complete, but not somatic continuity. This is the reverse of Darwin's position, and Weismann's victory over the conception of pangenesis marked the declining influence of Lamarckian theories of inheritance. As Weismann himself commented, "The transmission of acquired characters is an impossibility, for if the germ plasm is not formed anew in each individual but is derived from that which preceded it, its structure and above all its molecular constitution cannot depend upon the individual in which it happens to occur. . . ."[18] He also correctly recognized that sexual reproduction with its reshuffling of hereditary characters in every generation is really a remarkable device for promoting variability—new character combinations which may have selective value in the struggle for life. This observation was made possible by the slowly growing knowledge of cell mechanics to which the German workers of this period made such notable contributions.[19] So greatly does the sexual division promote new

[17] Op. cit., edition of 1889, p. 170.

[18] Ibid., p. 266.

[19] The advances in cell-staining techniques in Germany were responsible for major advances in cytology. Roux had observed

and individual combinations of characters that, without including any new mutations at all, it still contributes greatly to the potential evolutionary variability of any species.

Weismann's centering of emphasis upon a germ plasm out of which arose variation which was manifested in the living organism, and the failure of experiment to validate Darwin's pangenesis, led directly to the renewed experimentation which eventually culminated in the rediscovery of the lost work of Gregor Mendel. Before discussing the nature of that work, however, it is necessary to examine in a brief way just what Darwin, Wallace, and Weismann meant by variation. As we will see a little later, modern genetics, beginning with Mendel, has envisaged this problem differently from the way it was treated earlier in the century. The truth is that the Darwinists lumped under the term "variation" a great range of bodily differences about which they knew nothing whatever. They assumed that these characteristics were heritable—natural selection has no meaning without such inheritance—and that "variation and heredity," as Hogben says, "were coextensive processes."[20] Offspring were always a little different from their parents, the line of evolution was constantly in motion and constantly subjected to the selective attrition of the struggle for existence. As someone cleverly remarked, the species was always swallowing its tail. The normal curve of distribution for a given character was constantly being advanced on one side toward greater efficiency, and similarly suffering erosion from the side of the less effective. A stable species, in other words, was merely an il-

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the behavior of chromatin and examined mitosis. He believed that the secret of heredity was incorporated in a particulate manner within the nucleus. Following Roux's lead Weismann glimpsed the role of the chromosomes in carrying what today we would call genes. He also predicted in 1887 the reduction division which was later on to be established for meiosis.

[20] L. Hogben, *Genetic Principles in Medicine and Social Science*, New York, 1932, p. 167.

lusion created by the constant, slow pruning effect of natural selection.

This idea, in spite of other differences, is common to Darwin, Wallace, and Weismann. There was no clear comprehension that not all somatic variation is heritable. Thus the Darwinists tended to conceive of evolution as a continuous process. Even an organism which appears to be standing still, like some living fossils, is actually in a kind of dynamic balance. Its apparent resting state is really produced by the fact that selection is holding the norm of the species at a given spot instead of thrusting it forward. The modern interpretation of evolution and variation does not totally equate with this point of view. When we use the term "variation," our meaning is somewhat different from that of the Darwinists.

IV Artificial Selection and the Evolutionists

All through the earlier portion of the nineteenth century, and indeed the latter portion of the eighteenth century as well, evolutionists had had recourse to domesticated animals and plants as suggesting the mutability of biological form. Special creationists, even, had had to recognize a certain degree of plasticity in life whether wild or tame, but they had regarded this plasticity as being confined and demarcated. Species, *sammelarten*, as the Germans would say, were receptacles containing a range of varieties, but the species was the original created entity. The evolutionists, by contrast, had insisted that the species barrier was an illusion, that given time and opportunity the species, in Wallace's convenient phrase, would "depart indefinitely" from its original appearance. Buffon hinted at the possibility; Lamarck expressed it; Darwin used the whole process of artificial selection from which to develop, by analogy, his principle of natural selection. "The possibility of continued divergence," he remarked, "rests on the tendency in each part or organ

to go on varying in the same manner in which it has already varied; and that this occurs is proved by the steady and gradual improvement of many animals and plants during lengthened periods."[21] While Darwin was not unaware of what today we would call macro-mutations, or saltations, he was inclined to believe that in a state of nature, particularly, smaller changes operating by degrees were the main instrument of change.[22] Wallace, in a rather unguarded moment when he was attempting to counter the weight of the Jenkin-Bennett argument, speaks of the "powerful influence of heredity, which actually increases the tendency to produce the favorable variations with each succeeding generation. . . ."[23] The metaphysical implications of this remark are about as "unDarwinian" as some of Darwin's statements in this same period.

Neither Wallace nor Darwin had any experimental data which would enable them to distinguish between purely somatic, non-heritable variation and change of the genuine mutative variety. Darwin did have some notion of the complexities of inheritance, and it is not quite accurate to say that his notions of heredity were as simple as mixing water and ink. His knowledge, he well knew, was clouded and obscure:

"The germ . . . becomes a . . . marvelous object, for besides the visible changes to which it is subjected, we must believe that it is crowded with invisible characters, proper to both sexes, to both the right and left side of the body, and to a long line of male and female ancestors separated by hundreds or even thousands of generations from the present time; and these characters, like those written on paper with invisible ink, all lie ready to be evolved under certain known or unknown conditions."[24]

[21] Charles Darwin, *Variations of Animals and Plants under Domestication*, New York: Orange Judd & Co., 1868, Vol. 2, p. 300.
[22] Ibid., pp. 306–7.
[23] A. R. Wallace, "Natural Selection—Mr. Wallace's Reply to Mr. Bennett," *Nature*, 1870, Vol. 3, p. 49.
[24] VAP, Vol. 2, p. 80.

Arguments for a lessened antiquity for the globe began to mount as nineteenth-century physicists applied their calculations to the age of the earth. It is interesting to see that Darwin, who had once been quite casual as to time, shows an increasing interest in stories which suggest visible change in the present. He quotes, in the *Descent of Man,* the story of an American hunter who asserted that in a certain region male deer with single unbranched antlers were becoming more numerous than the normal variety. In reality the bucks were all yearlings with their first antlers, and the observer had been self-deceived.[25]

The story is less important than the glimpse it affords into Darwin's mind. Although he had written much about the minute, age-long increments involved in evolutionary change, it is clearly apparent that some of these apocryphal anecdotes possessed a strong appeal for Darwin. There was an understandable desire to show the process of evolution in operation, even as one tried to explain why it could not actually be seen. It is not surprising that Darwin occasionally succumbed to this temptation and was, in spite of a judicious temperament, a little too easily tempted by "spiked buck" stories. They fitted in well with his notions of the way in which domestic animals were altered. We come now, however, to a peculiar fact. It would appear that careful domestic breeding, whatever it may do to improve the quality of race horses and cabbages, is not actually in itself the road to the endless biological deviation which is evolution. There is great irony in this situation, for more than almost any other single factor, domestic breeding had been used as an argument for the reality of evolution. Its significance, however, is somewhat deceptive and capable of misinterpretation.

[25] J. T. Cunningham, "Organic Variations and Their Interpretation," *Nature,* 1898, Vol. 58, p. 594.

V *Mendel's Contribution*

In 1900 Correns, Tschermak, and De Vries, all working independently along the lines which Weismann and others had brought under examination, rediscovered the lost principles and lost paper of Mendel. The mere fact that three workers, after the long lapse of years, turned the little document up at the same time suggests that biological science was just reaching the point where Mendel's work could be appreciated. We have seen that Weismann had dealt with the germ plasm from "inside," that he did not accept pangenesis. Mendel, though cytological methods were unknown to him, had, years earlier, used essentially the same approach. By carefully controlled experiment he sought to trace particular characters of the adult through successive generations, to find out whether such characters remained the same, mixed, or disappeared. As he himself commented in the introduction to his paper, "Among all the numerous experiments made [prior to his time] not one has been carried out to such an extent and in such a way as to make it possible to determine the number of different forms under which the offspring of hybrids appear, or to arrange these forms with certainty according to their separate generations, or definitely to ascertain their statistical relations."[26] Bateson observed that these primary conceptions of Mendel were absolutely new in his day. There is a surgical precision about Mendel's procedures which is in marked contrast to the bunglesome anecdotal literature which fills so much even of Darwin's treatment of the subject. By selecting from a variety of pea plants a series of easily observable and identifiable characters, Mendel began his experiments with attention focused upon what happened to these characters in the course of their passage through several generations. The details of the experiments need

[26] Mendel's paper is reproduced in W. Bateson's *Mendel's Principles of Heredity,* Cambridge University Press, 1913.

not concern us here, but the results, from the standpoint of evolution, were spectacular.

Mendel had established for a series of plant characters the fact that they passed through the germ cell as *units.* Such units did not mix with other units, though it was found that certain characters might be suppressed in a heterozygous individual and re-emerge only in a homozygous one. All of these facts depended on gametic segregation. They had nothing to do with pangenesis, nothing to do with the kind of selection Darwin and Wallace had been largely concerned with. Jenkin's "swamping out" of a new mutant character could not take place so long as the individual had offspring. The units were particulate and unalterable except by actual mutation. A character could be carried and could be spread even if recessive. If it had survival value, its diffusion could be rapid.

Mendel challenged directly the Darwinian idea that cultivated plants had, in some manner, been made more "plastic" and variable. "Nothing," he says, "justifies the assumption that the tendency to the formation of varieties is so extraordinarily increased that the species speedily lose all stability." Instead of this assumption, Mendel draws upon his new discoveries to suggest that most cultivated plants are actually hybrids, mixing back and forth and showing the unit character ratios which such origins would suggest. The close proximity of domesticated forms promotes the opportunities for hybridism. Thus the fluctuating variability which Darwin sometimes attributed to the indirect factors of climate, soil, and other influences could not all be regarded as due to the emergence of new evolutionary characters. Much of the supposed new was old, but variable in its phenotypic expression. Mendel had shown that the vast array of living characteristics was controlled by mathematical laws of assortment, and biological units (genes) were transmitted independently. "The course of development," he remarked, "consists simply in this, that in each successive

generation the two primal characters issue distinct and unaltered out of the hybridized form, there being nothing whatever to show that either of them has inherited or taken over anything from the other."[27] Heredity and variation in the old Darwinian sense could, therefore, not be synonymous. The unit factors had a constancy which the Darwinians had failed to guess.[28]

VI Johannsen and Variation

We have seen that the Darwinian evolutionary mechanism was one involving the constant selection of small variations which were assumed to be numerous and inheritable. For a long time they were pretty much taken as given, and little or no attempt was made to determine what lay back of them, or whether all variation actually arose from the same cause. William Bateson, one of the first active Mendelian researchers, put the matter succinctly when he said: "The indiscriminate confounding of all divergences from type into one heterogeneous heap under the name 'variation' effectually concealed those features of order which the phenomena severally present, creating an enduring obstacle to the progress of evolutionary science."[29] It was Mendel's contribution to have revealed that not all variation was new in the sense of just emerging. Furthermore, the revelation that discrete unblending hereditary units existed which might be studied cytologically as well as through breeding experiments swung interest in new directions. Hugo De Vries, whom we shall discuss in the following chapter, seized public attention by his advocacy of rapid species alteration through sizable changes, speciation really, by sudden saltations or jumps. This doctrine in its extreme form was fated to be modified, but it cannot be denied that his em-

[27] Cited by Hugo Iltis, *Life of Mendel*, New York, 1932, pp. 147–48.

[28] Ibid., pp. 178–79.

[29] "Heredity and Evolution," *Popular Science Monthly*, 1904, Vol. 65, p. 524.

phasis upon the distinction between minor "fluctuating variations" and "discontinuous" variability, to which he applied the term "mutation," greatly stimulated research. Among the results of that research was the discovery of the Danish scientist W. L. Johannsen that the more or less constant somatic variations upon which Darwin and Wallace had placed their emphasis in species change cannot be selectively pushed beyond a certain point, that such variability does not contain the secret of "indefinite departure."

The Belgian anthropologist Lambert Quételet (1796–1874) observed in 1871 that for almost any biological character, height for example, one could erect a frequency distribution curve, provided a statistically adequate sample was available. There would be a scattering of individuals on either side of the norm and the extreme variants would lie at either end of the frequency curve. There is, in other words, an oscillation in a given population group around a mean value for any biological characteristic that we may choose to examine. It was this type of fluctuating variation which the Darwinian school had assumed might be "selected," either artificially or naturally, by the simple expedient of eliminating organisms at the lower end of the curve and selecting the individuals at the upper end of the curve for breeding purposes until the norm was moved forward. The breeder, it is true, can do certain things in this regard, but his effects are limited in a way the Darwinians were not in a position to foresee.

By selecting pure lines of beans, Johannsen anticipated that by raising beans from large bean seeds and from small and intermediate types he would obtain a series of different norms of size from his several plants. In this he failed. Whatever the size of the bean used, the progeny continued to fluctuate about a norm. Selection had had no effect in modifying the character of the norm. These variations in bean size were purely somatic, that is, they

had no connection with genetic factors, but instead apparently represented accidentally favorable or unfavorable growth conditions.

There is another factor which is concerned in the successful artificial breeding of both animals and plants. Johannsen did find that in spite of the somatic norm indicated by the frequency distribution of his pure lines of beans, there were also distinct means in separate lines of beans. This represented a true hereditary component. If we breed for large beans, say, or the fastest race horses, we are selecting out a stock which contains hereditary unit factors favorable to our intent. By constant selection we perfect a relatively pure line for the given effect we wish to produce. Through judicious mating we may even introduce new elements into the complex. Basically, however, our efforts are limited to what exists genetically in the stock. By careful manipulation we may draw certain characters to the surface or combine them with others.[80] We can, however, produce only what is potentially contained within a given line. Beyond this the breeder can do nothing but wait upon those incalculable events known as mutations, which appear spontaneously. For example, Johannsen at one point in his experiments observed that the range shifted in an unexplainable manner in one of his true lines. It was a true mutative event —a new factor had been introduced.

The result of Johannsen's studies of 1903 and later was to demonstrate conclusively (1) that organisms with the same *genotype* (i.e., genetic composition) could differ *phenotypically*, that is, in their physical appearance; (2) that the selection of phenotypic characters without a genetic base would not yield hereditary change; (3) that selection of hereditary characters could induce some degree of physical alteration but the effect would attenuate

[80] Raymond Pearl, "The Selection Problem," *American Naturalist*, 1917, Vol. 51, pp. 65–91.

and halt unless there were added mutations which are sometimes forthcoming and sometimes not.

For a time there was an understandable feeling that Darwinism was moribund. This was due partly to the discovery that certain of the variations upon which Darwin had depended were non-heritable, partly to the feeling that new changes emerged suddenly and were not the result of a slow accretion of characters. By degrees, however, the latter notion gave way. It began to be realized that there were small mutations as well as large, which would produce an effect not greatly different from the kind of continuous evolution Darwin had visualized. Thus the word "mutation" began to take on its modern meaning.[31] The word "macro-mutation" fits better today the kind of evolutionary leaps which, under De Vries's influence, were heavily popularized in the first few years of the twentieth century. In this period there was, for a brief time, a line drawn between the significance of large and small variations, but it was a line which could not be maintained.

As the century progressed, biological thought swung around to the opinion that however wrong Darwin may have been in certain details, he had been justified in his view that small changes are less apt to be detrimental to the organism and are the more likely mode of evolutionary change.[32] Nevertheless, in contemplating the Darwinian rejuvenation, it is well to remember a forgotten observation of Jacques Loeb, one of the finest experimental biologists of the early decades of this century. He commented that one of the greatest peculiarities of the Darwinian period was the seeming scientific indifference to the actual visible demonstration of specific change. The draft of

[31] T. H. Morgan, "For Darwin," *Popular Science Monthly*, 1909, Vol. 74, p. 375.

[32] H. J. Muller, "On the Relation Between Chromosome Changes and Gene Mutations" in *Mutation*. Report of Symposium held June 15–17, 1955, Brookhaven National Laboratory, Upton, N. Y., pp. 134, 142.

limitless time at the Darwinists' command led them to assume that the process was too slow to be observed at all. That this troubled Darwin, particularly after the time scale began to be shortened, we can see from stories such as the account of the spiked buck. The literature, however, remained largely polemical. It was therefore an enormous leap forward when Hugo De Vries proposed his "mutation" theory and demonstrated hereditary changes of form. The rediscovery of Mendel at this time with his evidence for the actual existence of specific hereditary determiners marked, as Loeb says, "the beginning of a real theory of heredity and evolution." Even though some of De Vries's thought was later to be repudiated, and though Loeb was writing in the period of uncritical enthusiasm for De Vries's discoveries, we may, I think, with little reservation, endorse this final remark: "If it is at all possible to produce new species artificially I think that the discoveries of Mendel and De Vries must be the starting point."[33]

In the next fifty years Mendel's principles were expanded to cover many organisms, both plant and animal. Mathematical tools elaborated by such men as Fisher, Sewall Wright, and others were introduced to handle the theoretical genetics of entire populations. It was discovered that certain types of mutations occur over and over again in particular stocks, and thus by inference it was possible to assume that a certain reservoir of variability was always at hand in particular species—a reservoir possibly contributing to organic change in times of shifting conditions. Certain kinds of genetic mutation were found more likely to occur than others.[34]

Cytology continued to press farther and farther into the

[33] "The Recent Development of Biology," *Science*, 1904, n.s. Vol. 20, p. 781.

[34] Thomas Hunt Morgan, "The Bearing of Mendelism on the Origin of Species," *Scientific Monthly*, 1923, Vol. 16, p. 247. See also W. E. Castle, "Mendel's Laws of Heredity," *Science*, 1903, n.s. Vol. 18, p. 404.

mysterious mechanics of the nucleus and the cytoplasm. Finally, today, mutations are being artificially induced by various types of radiation and chemical agents. All this, however, is a book-long story in itself. There is still much that is unknown: the cellular location and nature of the great mechanisms that control the structure of phyla and classes escape us still; we know far more about fruit flies than men. It is strange, now, to walk through the laboratories and encounter the warning signs before radiation experiments, and to think of Mendel among the droning bees and flowers in the monastery at Brünn. "My time will come," he had said to his friend Niessl. "My time will come." Perhaps, as others had heard the sound of change and the flow of waters in the night, Mendel had learned from those tiny intricate units that shape a flower's heart something of the elemental patience that holds a living organism to its course while mountains wear away. "My time will come," he said. It was the indefinable echo of another century in the air.

PART IV

BEYOND THE ORIGIN
The Modern Synthesis

Stebbins, G. Ledyard: *Processes of Organic Evolution*, Chapter One

Chapter 1

The Synthetic Theory of Evolution and Its Development

Modern biology has two unifying concepts. One is the concept of organization. This tells us that at every level, from the molecule through the supra-molecular organelle, the cell, the tissue, the organism, the individual, and up to the population or the society, the properties of life depend only to a small degree upon the substances of which living matter is composed. To a much greater degree living things owe their nature to the way in which the components are organized into orderly patterns, which are far more permanent than the substances themselves. The other unifying concept of biology is that of the continuity of life through heredity and evolution. This tells us that organisms resemble each other because they have received from some common ancestor hereditary elements, chiefly the chromosomes of their nuclei, which are alike both in respect to the substances which they contain and the way in which these substances are organized. When related kinds of organisms differ from each other, this means that in the separate lines of descent from their common ancestor changes in the hereditary elements have taken place, and these changes have become established in whole populations.

The Fact of Evolution

At the outset we should realize that the great majority of biologists accept as demonstrated the fact that organisms have evolved. To be sure, no biologist has actually seen the origin by evolution of a major group of organisms. Nevertheless, races and species have been produced by duplicating in the laboratory and garden some of the evolutionary processes known to take place in nature. The reason that major steps in evolution have never been observed is that they require millions of years to be completed. The evolutionary processes which gave rise to major groups of organisms, such as genera and families, took place in the remote past, long before there were people to observe them. Nevertheless, the facts which we know about these origins, some of which will be discussed in Chapter 7, provide very strong circumstantial evidence to indicate that the processes which brought them about were very similar to those found in modern groups of animals and plants which are evolving all around us today.

The state of our knowledge about evolution depends upon the level being considered. The origin of races and species by evolution is a demonstrated fact, supported by experimental evidence as strong as the evidence for the existence of atoms, electrons, protons, and other particles of matter. The evolution of major groups such as dinosaurs, horses, and primates, including mankind, is documented in each case by a long series of fossils, the age of which is known with reasonable accuracy. Evolutionary relationships between living groups are supported further by strong and detailed resemblances in form, patterns of development, and, particularly, the structure and behavior of their macromolecules, such as nucleic acids and proteins. Our knowledge of these major steps of evolution is much like that of our knowledge of ancient history. We do not have any reliable eye-witness accounts of the events which produced the rise and fall of the civilizations of ancient Egypt, Sumeria, Babylon, and Crete, and the contemporary written records of these ancient times are fragmentary and unreliable. Nevertheless, the indirect evidence that these civilizations existed is so strong that it is accepted by scholars and laymen alike. Moreover, we teach as historical fact many of the probable events connected with their rise and fall. The evidence which biologists now have about the rise and extinction of major groups of animals in past geological eras is of a very similar nature, and carries with it about the same degree of high probability.

With respect to even earlier events, such as the origin of vertebrate animals, the differentiation of the animal kingdom into major evolutionary lines or phyla, the origin of the cell structure of higher (eukaryote) organisms, and the origin of life itself, our degree of certainty is considerably less. Nevertheless, scientific reasons exist for this lack of certainty, and gaps in our knowledge are being filled in various ways. As explained in Chapter 7, the chance that a particular kind of organism will be preserved as a fossil depends greatly upon its structure. Small, soft-bodied organisms are far less likely to be preserved than

large ones, or those that possess hard, indestructible shells or other coverings. Knowledge of modern forms indicates strongly that the ancestors of fishes and other vertebrates, as well as the earliest many-celled animals, were small and soft-bodied; thus, their absence from the fossil record is not proof that they never existed. Furthermore, the older the geological formation, the more likely it has been warped, subjected to excessive heat, or worn away by stream erosion since it was formed. Age itself, therefore, is a powerful factor in reducing the probability that a particular fossil will be preserved. To obtain information about the earliest events of evolution, the scientist must look for whatever evidence he can find, and piece fragments together in much the same way as a detective attempting to solve a crime.

Extrapolation, Faith, and Belief

The key to understanding events of the remote past is EXTRAPOLATION. This is a method by which scientists, and others, extend known data into an area that is not known. It depends upon the validity of certain assumptions. Evolutionists assume that the world of 100 million, 200 million, or even 500 million years ago was much like the world of today, except that it was inhabited by different kinds of animals and plants that are now extinct. Careful studies of geological formations of all ages show that mountain building, degradation through erosion, the rise and extinction of volcanoes, the flow of rivers, and the coming and passing of glacial epochs, have taken place repeatedly throughout the past, so that the physical features of the earth, as well as its atmosphere and storms, have always been much as they are today. There have been, of course, variations in the amount of land relative to the seas, the extent and height of mountain ranges, the dryness or wetness of the climate, and so on. Equally careful comparisons of the molecular composition, genetic structure, cell biology, and similar features of organisms as diverse as one-celled protozoa, seaweeds, ferns, flowering plants, jellyfishes, worms, insects, fishes, mammals, and man have shown that they are all alike with respect to the basic structure and composition of their proteins and genes. Basic cellular processes such as respiration and protein synthesis are also similar. These comparisons form the basis for the assumption that populations of organisms living in the remote past had genetic structures, and capabilities for stability or change, essentially similar to those that can be studied directly in modern populations. The extrapolations made by the evolutionist from the present to the remote past are based on the assumption that the basic properties of life have been similar throughout the time span since living organisms first appeared, and that quantitative differences from present conditions can be discovered by studying the structure and chemistry of ancient rock formations.

If it is based upon an insufficient factual basis, extrapolation can be dangerous. For instance if a baby, one year old, weighs three times as much as

it did when born, and if no other facts were available, one might reach the absurd conclusion that it would treble its weight every year, and so, at five years, would weigh about 2000 pounds! If, however, one had accurate records of the annual increase in weight of both parents, of aunts and uncles, and of brothers or sisters, plus comparisons of the diets of these relatives with the expected future diet of the baby, one could extrapolate with reasonable accuracy the child's weight at various future ages.

Extrapolation is an accepted scientific method. It is the only possible method in astronomy, and has led to very accurate predictions of eclipses. It is commonly used in geology. Not only has the history of the earth been revealed to a large extent by extrapolation; in specific situations valuable mineral deposits and oil fields have been discovered by extrapolating from the facts emerging from careful studies of surface geology. In political science, extrapolation from insufficient facts produced the famous misprediction by the *Literary Digest* of the 1936 American presidential election; but recent predictions of elections, based upon computerized syntheses of large numbers of facts, have been surprisingly accurate.

In addition to the factual evidence reviewed in this book, scientists have three reasons for accepting evolution as one of the cornerstones of modern biology. First, it serves as a focus by which facts from such widely divergent fields as paleontology, comparative morphology and anatomy, biogeography, ecology, genetics, physiology, cell biology, and biochemistry can be related to each other to form an integrated whole. One eminent biologist, Th. Dobzhansky, has stated "nothing in biology makes sense without evolution." Second, knowledge about evolution gives one a perspective about the nature and possible future of the modern world that can be obtained in no other way. This topic is discussed further in the last chapter of this book. Finally, evolution is the only scientific explanation of the origin of the millions of different kinds of animals, plants, and microorganisms that surround us. To be sure, some recent critics of evolution have maintained that a scientific theory of special creation can exist. They support their claim chiefly by stating "evidence" which, in their opinion, makes it difficult or impossible to believe in evolution. They cannot, however, provide positive evidence in favor of special creation, or analyze how a creator might have performed his miracles. Special creation can be accepted only as an act of faith in the inviolable truth of a written word, which in most of the western world is the Bible. Certainly, some degree of faith is necessary in order to accept evolution as the way in which events of the remote past, such as the origin of life, took place. However, this is not blind faith in unquestioned authority. It is, on the other hand, a continually questioning faith. It asserts that doubts can be slowly and gradually removed by new factual discoveries, which, in turn, will generate new ideas. The explosive advance of scientific knowledge during the past century has fully justified this kind of scientific faith.

Since Darwin developed his theory of evolution more than a century ago, biologists have studied this subject in two different ways. Some have been

interested in the course of evolution. By comparing a multitude of different kinds of animals or plants, they have tried to work out the evolutionary family tree of some particular group, such as the horses, the cone bearing trees, or mankind. Other biologists have asked themselves the question: "What makes evolution go?" By means of observations and experiments of various sorts on populations of living organisms, they are learning about the processes of evolution and the mechanisms responsible for them. The present book will consider only this second approach to the study of evolution. The study of the course of evolution, or phylogeny as it is often called, must be carried out in a somewhat different way in each separate group of organisms. Such studies have yielded few general principles which apply equally well to all kinds of living things. On the other hand the processes of evolution are in many ways similar even when we compare such different forms as bacteria, flies, grasses, and mammals. Consequently, an understanding of these processes is of far greater importance to the general biologist than is knowledge of the particular ancestry of any group.

The Modern Synthetic Theory of Evolution

The modern, synthetic theory of evolution recognizes four basic types of processes: GENE MUTATION, CHANGES IN CHROMOSOME STRUCTURE AND NUMBER, GENETIC RECOMBINATION, and NATURAL SELECTION. The first three provide the genetic variability without which change cannot take place; natural selection guides populations of organisms into adaptive channels (Figure 1.1). In addi-

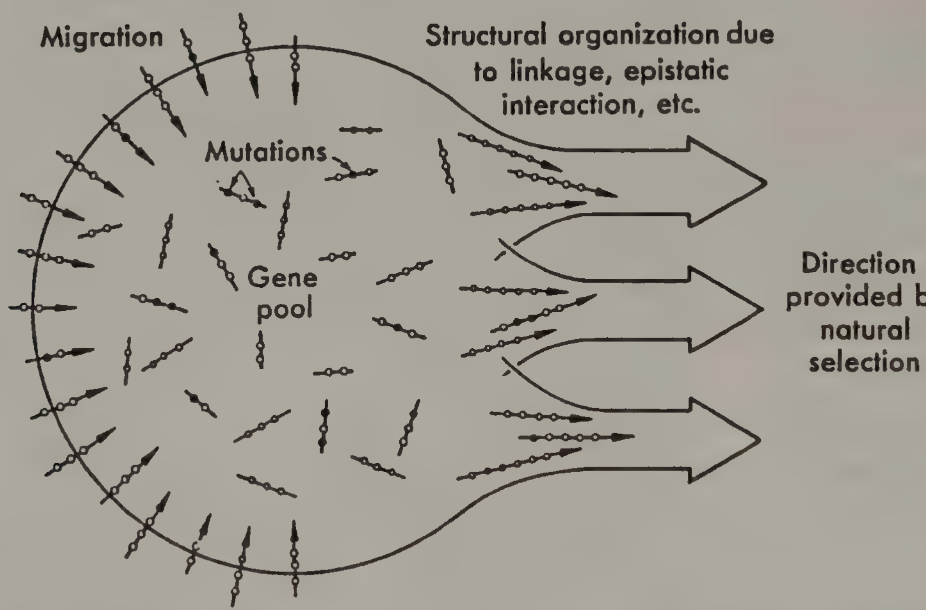


Fig. 1.1 Diagram to illustrate how the four basic processes—(1) mutation; (2) genetic recombination, which results from intercrossing between individuals of the population as well as between them and occasional new genotypes which enter by migration; (3) structural changes in the chromosomes, which affect linkage and epistatic interaction of genes; and (4) natural selection—interact to produce a progressive change in the population which keeps it adapted to the changing environment.

tion, three accessory processes affect the working of these four basic processes. MIGRATION of individuals from one population to another, as well as HYBRIDIZATION between races or closely related species both increase the amount of genetic variability available to a population. The effects of CHANCE, acting on small populations, may alter the way in which natural selection guides the course of evolution. The purpose of the present book is to review our knowledge of each of these processes, and to show how they are interrelated with each other. The more we know about the four basic processes, the less reason we have for believing that any other basic processes remain to be discovered. We do not need to search any more for hidden causes of evolution. Nevertheless, we do need to understand much more about the way in which known processes interact with each other.

At the outset we must recognize that at least in higher organisms, and perhaps in microorganisms as well, the three processes, mutation, genetic recombination, and natural selection, are equally indispensable for evolutionary change to take place. Speculations as to which of the three is the most important are completely pointless. The best way to understand their interrelationships is to recognize that all populations of sexually reproducing organisms contain a large "gene pool" of genetic variability. Like a natural pool of water, the gene pool maintains a dynamic equilibrium between inflow and outflow of genes, and may become larger or smaller, depending upon various external and internal factors. Genes may be added to the pool (1) by immigration from other gene pools, which requires crossing or hybridization between immigrants and old residents of the population; or (2) by mutation, followed by spread of the mutant allele through the population. Genes are removed from the pool chiefly by (1) natural selection, which constantly cleanses the pool of unfavorable mutations and builds up adaptive complexes of genes, and (2) chance elimination of alleles, which takes place in small populations or during reductions of population size. Genetic recombination, following the principles of Mendelian heredity, is constantly reshuffling the genes in the pool, presenting new combinations for acceptance or rejection by natural selection. Its importance lies in the fact that adaptiveness of an individual rarely if ever depends upon the independent action of individual genes or gene mutations. Due to constant interaction between genes at different loci, or EPISTASIS, the adaptive value of most genes that are retained in populations depends upon their ability to form favorable combinations with other genes.

Natural selection, which results from interactions between populations and their environment, may either stabilize gene composition by eliminating most or all immigrants and mutants, or change it in various ways. Evolution takes place through alterations of the frequency of genes and gene combinations in the population, brought about by natural selection. Finally, reproductive isolation, which includes all the barriers to gene exchange between populations, has a canalizing effect. Since the richness and organizational complexity of the gene pool make possible several different responses to the same kind of environ-

mental change, populations that are reproductively isolated from each other are almost certain to evolve in different directions, while those that are not so isolated because of gene exchange, will evolve in the same direction.

Charles Darwin, the Founder of Evolutionary Theory

The synthetic theory of evolutionary dynamics just outlined was not thought up by any one scientist. Rather, it has itself evolved during the last century through an accumulation of factual evidence and theoretical conclusions. We can begin its history with the work of Charles Darwin. To be sure, a number of naturalists and philosophers, beginning with the ancient Greeks, had thought of the possibility that the different forms of life have evolved from each other. The most important of these before Darwin's time was Jean Baptiste Lamarck, a renowned French naturalist, who in his later years produced a well-known theory of evolution. It was based largely upon the concept that modifications which the organism acquires in adaptation to the environments which it meets during its lifetime are automatically handed down to its descendants, and so become part of heredity. For instance, Lamarck believed that the giraffe had acquired its long neck because its ancestors had stretched their necks to reach the leaves of tall trees. As a result of this exercise, the muscles and bones of the neck became abnormally developed. The effects of this development were believed to have been transmitted somehow to the descendants of these neck-stretching ancestors, and so to have become a permanent hereditary trait of the giraffe (Figure 1.2). In a similar way, a Lamarckian theorist would explain the dark skin color of some races of man by assuming that the ancestors of these races had been exposed repeatedly to the strong rays of the tropical sun, thus acquiring a tan which was transmitted to their descendants. This concept of the inheritance of acquired modifications is now completely disproved. Although Darwin and his contemporaries did not have enough knowledge to reach this conclusion, most of them paid little attention to Lamarck's theory because it consisted entirely of armchair speculation, and Lamarck produced no factual evidence to support it.

Charles Darwin's approach to the theory of evolution was quite different from that of Lamarck. His life was devoted to a continuous series of observations, experiments, and accumulation of facts by correspondence with other naturalists. All of his efforts were directed toward a better understanding of the adaptation of organisms and their evolution. He began the observations which led to his theory of evolution at the age of 22, when he was naturalist on *H.M.S. Beagle,* a ship which the British navy sent on a five year cruise around the world. The book which Darwin wrote about this voyage, now a classic, is fascinating reading for anyone interested in natural history. At the same time it gives us valuable insight into the kinds of observations which led Darwin to his

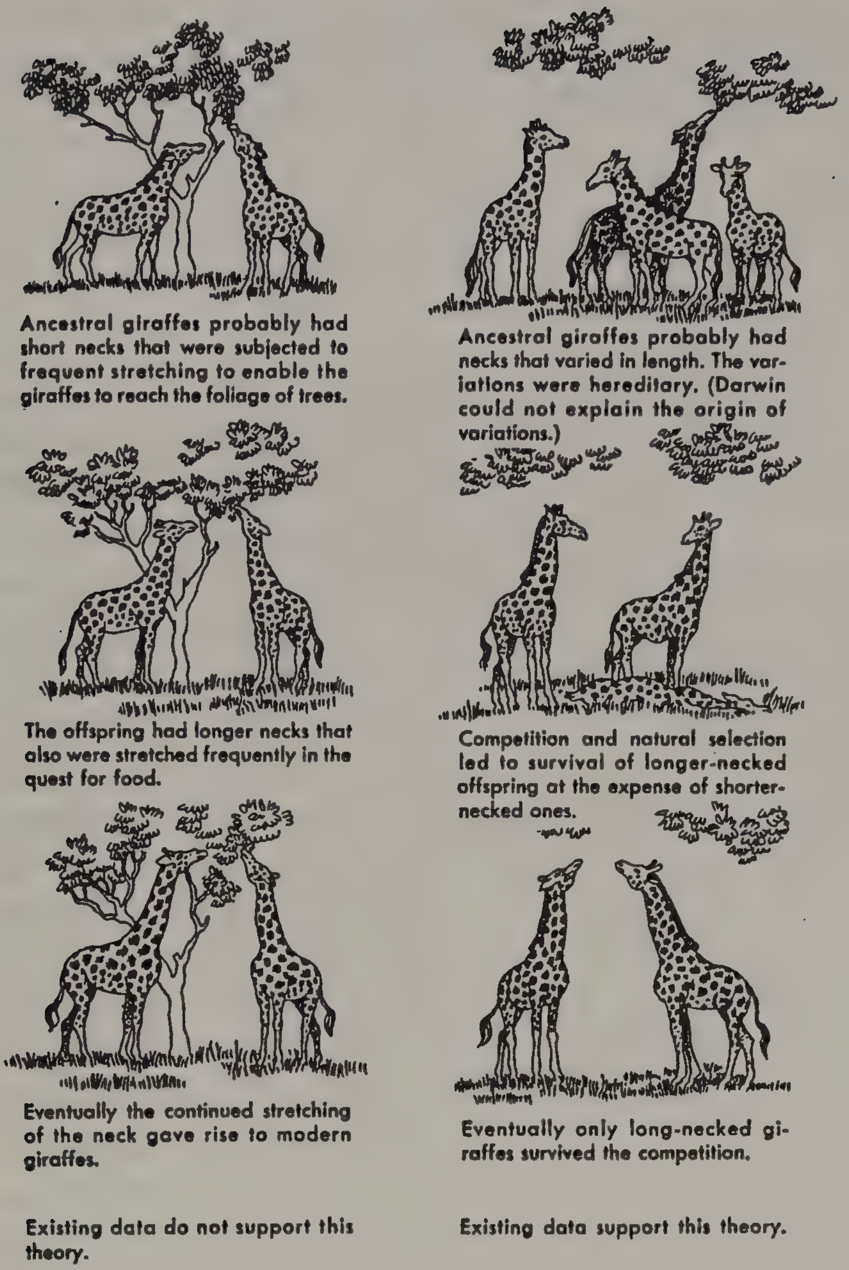


Fig. 1.2 Illustration showing how the origin of the giraffe's long neck is explained according to the now discredited Lamarckian theory of the inheritance of acquired modifications and according to the generally accepted Darwinian theory of natural selection. From J. A. Moore, *Biological Science: An Inquiry into Life* (Harcourt Brace and World).

theory. During an excursion into the Argentine pampas from the city of Buenos Aires he became greatly impressed with the revolutionary change in the country's vegetation which had been produced by the arrival of civilized man from Europe. Immigrant species of plants brought in by accident from their native European home were overrunning the fields and roadsides driving out the native South American species. Later, the *Beagle* sailed down the barren shores of Patagonia, near the southern tip of South America, where Darwin saw some of the richest fossil beds in the world. The bones of extinct species of mammals were lying exposed on the cliffs by the thousands, giving ample evidence that the animals of past ages were different from those of present-day South America but clearly related to them.

After passing through the Straits of Magellan the *Beagle* sailed northward along the Pacific coast of South America, and spent five weeks at the Galápagos Islands, 600 miles west of the coast of Ecuador. Here Darwin became aware of the fact that the principal animals were different from those of the South American coast. Huge lizards were everywhere, some of them living on the

actual seashore and feeding on marine life. These lizards are peculiar to the Galápagos, but their nearest relatives are found in South America. The giant tortoises for which the islands are named were the commonest animals of the interior of the islands. Not only do these belong to a completely different group from any inhabiting the American mainland, but in addition each separate island of the Galápagos archipelago has its own particular race of tortoise (Figure 1.3). Darwin observed that these races of tortoise are so different from each other that even the sailors who often visited the islands could tell by its appearance from which island a particular tortoise came. The plant life is distinguished by the fact that the largest and commonest trees of the interior forests belong to a distinctive genus (*Scalesia*) of the sunflower family (Compositae). In other parts of the world this family produces only herbs and small shrubs. Like the tortoises, these tree sunflowers include a separate race or species for almost every one of the islands. In the book which he wrote about his journey Darwin comments on these facts as follows:

> Why, on these small points of land, which within a late geological period must have been covered by the ocean, which are formed of basaltic lava, and therefore differ in geological character from the American continent, and are placed under a peculiar climate,—why were their aboriginal inhabitants, associated, I may add, in different proportions both in kind and number from those on the continent, and therefore acting on each other in a different manner—why were they created on American types of organization?

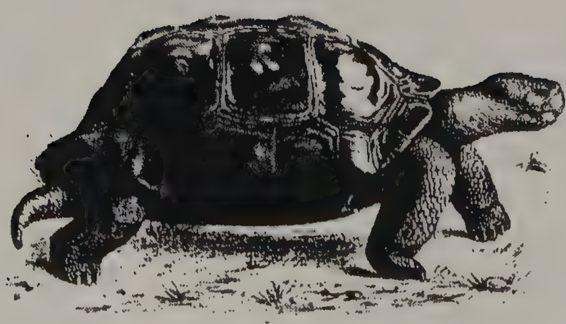
And later:

> Reviewing the facts here given, one is astonished at the amount of creative force, if such an expression may be used, displayed on these small, barren, and rocky islands; and still more so, at its diverse yet analogous action on points so near each other.

From these comments we can see that in 1837, when he was 28 years old, Darwin was already questioning the then prevalent doctrine of special creation. A year later (1838) he read a book on human populations by the English clergyman, Thomas Malthus, in which the author pointed out that unless checked by disease, war, famine, or conscious control of reproduction, the number of people on the earth would in a short time increase so much that there would be "standing room only." Darwin could easily obtain figures to show that the same would be true of any kind of animal or plant, even for such slowly reproducing species as the elephant. As a naturalist, he was well aware of the fact that organisms are adapted to their environment, and that this adaptation often takes the form of elaborate and bizarre structures and activities. By careful observation of many species in nature, in his garden, and as animals kept in cages about his home, he convinced himself that the individuals of any popu-

Abingdon

Duncan



Albemarle

Fig. 1.3 Drawings showing the characteristics of three different species of tortoises found on different islands in the Galápagos. The longer necked species live in relatively dry places and feed on tree cacti; the species with the short, straight neck lives in moister regions and feeds on dense, low growing vegetation.

lation differ slightly from each other in many characteristics, including those which contribute toward adaptation. He made the logical deduction, therefore, that the factors which check the increase of numbers in a species act more strongly on those individuals which are relatively poorly adapted and favor those which are best fitted to their environment. Since these favored individuals will leave more offspring than their less well adapted associates, this process of natural selection, continued over many generations, should evolve ever more perfect and complex adaptations, and so bring about progressive evolution.

Many scientists, as soon as such a fine idea occurred to them, would immediately rush to print with it. But this was not Darwin's way of working. He started his first notebook on the transmutation of species in 1837, and in 1844 wrote his first essay on the subject. He never published this essay because he felt that he did not have enough evidence for his theory. Instead, he devoted his entire attention to accumulating systematically the necessary evidence. Having inherited a fortune, he could live in his country home and devote his entire time to gathering all kinds of information which might bear upon his theory. He realized that natural selection, as he conceived it, is very much like artificial selection, by means of which animal and plant breeders had been able to produce much altered and improved breeds of domestic animals and cultivated plants. He therefore became a pigeon breeder and studied carefully both the way in which the fancy breeds of his day had been produced, and the anatomical characteristics which distinguished them from each other and from wild pigeons. He chose the pigeon because all domestic varieties of this bird are certainly derived from a well-known wild species of Europe. Darwin was astonished to discover that in certain anatomical features the breeds of pigeons differ from each other to a greater degree than do many species and even families of wild birds (Figure 1.4). This convinced him that selection, either artificial or natural, if continued long enough and with great enough intensity, could bring about the kinds of differences by which naturalists are accustomed to recognize various wild species.

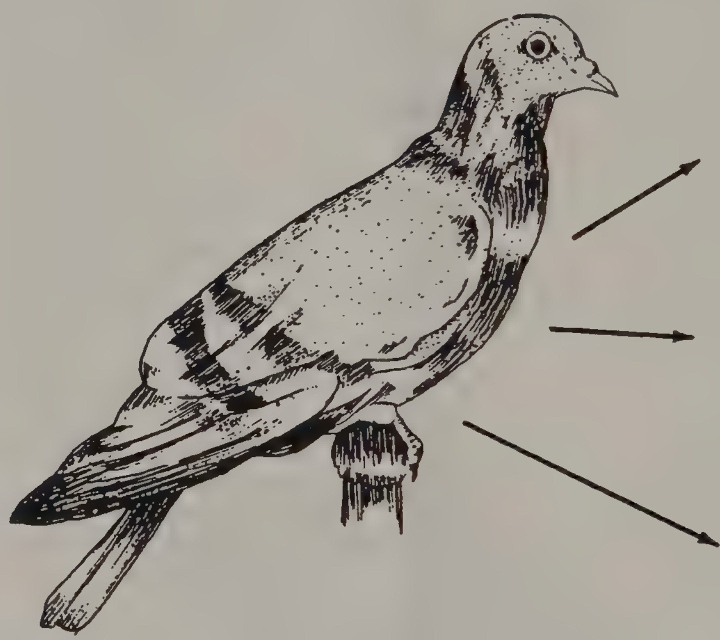
At the same time, Darwin was gathering facts of many other kinds which might bear on his theory. Through his own observations of fossil animals, as well as by studying the publications of contemporary zoologists and paleontologists, he learned much about prehistoric animals and their relationships with modern species. Sir Joseph Hooker, an equally eminent botanist, supplied him with valuable evidence from the plant kingdom.

Twenty years after his discovery of Malthus' book Darwin was still gathering facts for a large and complete treatise of his own when he received a manuscript from Alfred Russell Wallace, another British naturalist who was at that time studying the fauna of the East Indies. In this manuscript, Wallace set forth clearly the same theory as Darwin's, which he had conceived independently: that species of animals have evolved from each other through the action of natural selection. Rather than competing with each other to be the first to

publish this theory, Darwin and Wallace agreed that their papers should be read jointly at an historic meeting of the Linnean Society of London, on July 1, 1858. A year later (1859), Darwin published his famous classic, *The Origin of Species,* which, though much shorter than he had originally intended it to be, nevertheless contained a great wealth of factual material.

Both biologists and other people reacted immediately and violently to this book. Some found in it answers to questions which they had long been asking themselves; others defended tenaciously their previous concepts about the immutability of species. The criticism from the church, on the grounds that Darwin's theory contradicts the story of creation told in the Book of Genesis, led to violent polemics in Darwin's day and have continued into the present century.

Darwin took most seriously those criticisms which were levelled at his theory of natural selection. In successive editions of *The Origin of Species* he spent many words answering these critics. We usually read the sixth edition, published in 1872, which contains all of these answers. At the same time, Darwin was continuing his research in a variety of directions. The natural history of earthworms, the forms of flowers in relation to their methods of pollination, the effects of cross- and self-fertilization in plants, the differences between males and females of the same species; all these he studied carefully in order to find an explanation of their origin based upon natural selection. Reviewing the life of Darwin, we cannot fail to admire the breadth of his knowledge, the scope of his investigations, and the persistence with which he directed these toward a single goal. Darwin succeeded in convincing the world of the existence and great significance of organic evolution because of his profound knowledge of natural history; his ability to accumulate a wide variety of facts by means of observation, experiment, and correspondence with other naturalists; and particularly his ability to synthesize these facts into a coherent whole. Another important factor was that the naturalists of the mid-nineteenth century, who were finishing the most intensive series of explorations of the world's flora and fauna which has ever been made, were in the right mood for seeking and accepting explanations for the tremendous diversity of living things which was now laid before them.



Wild Rock

Fig. 1.4 Variation among the breeds of domestic pigeon, a subject of investigation by Darwin which confirmed for him the strong influence on variation which can be exerted by natural selection. From Wallace and Srb, *Adaptation* (Prentice-Hall, Inc.).

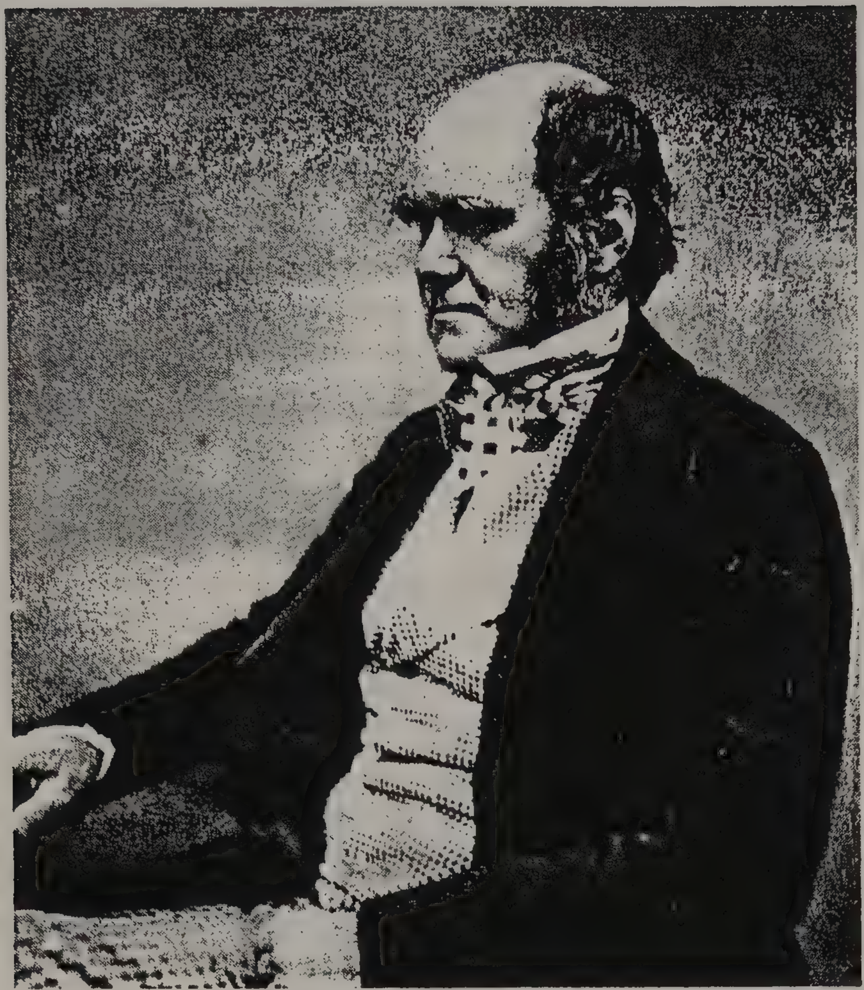


Fig. 1.5 Photograph of Charles Darwin in middle age. From C. Darwin, *Foundations of the Origin*, F. Darwin (ed.). Reprinted by permission of the publisher, Cambridge University Press.

The Impact of Mendelism

Nevertheless, Darwin's theory had one serious flaw. He knew nothing about the causes of hereditary variation, and his opinions on this subject were neither logical nor consistent. At times he accepted, and in other writings he rejected Lamarck's notion of the inheritance of adaptations acquired during the lifetime of the individual. Along with most practical animal breeders and students of human heredity of his day, he regarded the hereditary substances as fluid in nature, and the observed intermediate nature of hybrids between races or breeds as resulting from a mixture of parental fluids in their bodies. One of Darwin's severest critics, Fleeming Jenkin, pointed out that selection could not sort out superior fluids from a mixture, and so, according to prevailing theory, could not be the means by which superior types could be derived from crosses between breeds. Because he knew so little about heredity, Darwin could not provide a satisfactory answer to this criticism.

The answer, that heredity is determined not by fluids but by particulate genes, already existed in the garden of an obscure monastery in Brunn, Czechoslovakia, in the experiments of Gregor Mendel. But Darwin knew nothing about this.

Furthermore, the rediscovery of Mendel's laws of heredity by Correns, de Vries, and Tschermak in 1900 did not immediately reinforce Darwin's theory,

but on the contrary, placed it in a temporary eclipse. This was because both Mendel and the rediscoverers were studying characteristics which, as differences between natural populations, are relatively uncommon. Mendel crossed a tall with a dwarf strain of peas and found in the second generation a ratio of three tall to one dwarf plant. He could, therefore, conclude that the parents differed in respect to a single gene controlling size. When we cross a tall human being with a short one, or a tall race of wild yarrow with a dwarf alpine plant of the same species, we find that no simple Mendelian ratio can be found in the second hybrid generation. The difference between tallness and shortness in these species is governed by many genes, each one of which has only a slight effect on size. Darwin's theory was based upon his sound observation that most differences between natural populations are quantitative in nature, but neither he nor the earliest of the Mendelian geneticists understood why this is so.

Two other events in the early history of genetics combined to reinforce the skepticism of these geneticists toward Darwin's theory. The first of these was the discovery by de Vries that in the evening primrose (*Oenothera*) new types, differing markedly from their parents in a number of characteristics, can arise at a single step. He called these changes mutations, a term which has ever since been used chiefly for changes in single genes. We now know that many mutations occur which are not abrupt alterations of one or many characteristics, but produce slight, barely perceptible modifications of the visible structures. In 1905, a few years after the work of de Vries, the Danish botanist, Johannsen, tried applying Darwin's theory to altering the genetic nature of the garden bean. He selected the largest and the smallest beans from the seed lot of a single variety, and grew offspring from them. In the first generation, the larger beans produced slightly larger offspring than the smaller ones, but in later generations selection for large and small size had no effect on the offspring. From this experiment, Johannsen and other early geneticists concluded that the fluctuating variation which Darwin had observed in natural populations, and which he considered to be the basis of natural selection, was actually not hereditary at all, but merely due to the effect of the environment on individual organisms. Putting together the discoveries of de Vries and Johannsen, they argued that evolution takes place through the spontaneous origin of new types, which differ radically from their parents in several characteristics. Natural selection, according to them, has merely the negative function of eliminating those types which are unfit to survive.

This hypothesis, which was known during the first quarter of the twentieth century as the mutation theory, has not withstood the test of time for a number of reasons. The mutations which de Vries found in the evening primrose were later found to be not the result of new genetic variation at all, but merely a peculiar type of genetic segregation due to the fact that this plant has a very anomalous type of chromosome behavior. Later on, Morgan and his associates found true mutations in the fly, *Drosophila*, which are actually spontaneous alterations of genes, and they have since been found in a large number of

different organisms. But nearly all mutations which produce large, conspicuous changes also make the organisms bearing them weaker and unable to compete with their unchanged associates. Moreover, geneticists have recently carried out experiments on selection for size and other characteristics with mice, flies, corn, and other organisms, and have obtained entirely different results from those which Johannsen got in his experiments with beans. Selection in these organisms has produced progressive changes over as many as fifty to a hundred generations. This difference is explained by the fact that the garden bean is self fertilizing and has been selected by breeders over many generations for uniformity and constancy. In this way, differences due to genes with small effects have been artificially eliminated.

In natural populations, most of which are cross fertilizing and have not been subjected to such rigid selection, a large "gene pool" of genetically controlled variation exists at all times. Most of the adaptively important mutations do not produce entirely new types, but merely add quantitatively to the gene pool for already existing variations. Natural selection has the positive, creative function of sorting out a few adaptive gene combinations from the infinite number of possibilities inherent in the gene pool.

The numerous facts which are the basis of the statements just made were acquired by several geneticists during the entire first half of this century. H. Nilsson-Ehle in Sweden and E. M. East at Harvard showed that quantitative hereditary variation is due to the simultaneous action of many separate genes, each of which has a small effect by itself. J. B. S. Haldane and R. A. Fisher in England, Sewall Wright in the United States, and S. S. Chetverikov in the Soviet Union all showed by mathematical calculations that evolutionary change must depend not only on the origin of genes with new effects, but also on changes in the frequency of all of the genes in the population. Such changes cannot be brought about by mutation alone, with selection acting only to eliminate unfit mutants, but must depend upon the continuous action of natural selection. acting at measurable intensities. Finally, various geneticists developed techniques for raising large populations of drosophila flies of known genetic composition in cages under carefully controlled environments. In this way, a tremendous wealth of experimental evidence has been amassed in favor of the theories of population dynamics and evolution worked out mathematically by Haldane, Fisher, Wright, and Chetverikov. Thus the modern, synthetic theory of evolution has acquired a solid basis of scientific fact.

The Conflict between Darwinism and Mendelism, and Its Resolution

One of the most curious phases in the history of modern biology is the violent conflict concerning the nature of hereditary variation and the processes of evolution which took place between the early Mendelians, chiefly de Vries

Bateson, and Johannsen, and the contemporary Darwinian naturalists, such as David Starr Jordan and H. F. Osborn, as well as statistical biologists such as Francis Galton and Karl Pearson. Its cause was two-fold. In the first place, the members of the two opposing camps were biologists with opposing temperaments and philosophical attitudes. De Vries, Bateson, and Johannsen were basically experimentalists, to whom precision in experimental design and care in interpretation of results were of prime importance. Because their field was young, they could maintain these standards only at the expense of breadth, so that they had to base generalizations on a few examples. The naturalists were already aware of a fact which these experimentalists did not realize, and which became obvious only during the subsequent twenty years. This fact is that the examples of simple genetic segregation and constancy which Mendel, de Vries, and Johannsen found in their experiments were not representative of hereditary variation as it exists in natural populations of cross breeding organisms. On the other hand, the naturalists who promoted Darwin's theory in the early part of this century were describers and cataloguers who had no conception at all of the precision of thinking which is required to design a good experiment and to interpret its results correctly. Consequently, they failed to appreciate the significance of either Mendelian genetics or the mutation theory, or to understand how these concepts could be modified to interpret the pattern of variation in nature, which they knew very well.

The conflict was caused also by the different outlook of the two groups on variation itself. The Mendelians were looking upward from the genes, the naturalists downward from the phenotypes, and neither had the least conception of the enormous complexity of biological processes which separates the two in higher animals and plants. This complexity is illustrated in the following diagrams. The first of them (Figure 1.6) illustrates two empirically demonstrated facts and their probable explanation. One of these which has already been mentioned, is that most visible differences between populations, races, and species of higher animals and plants are governed by many different genes, each of which contributes to a different one of the numerous metabolic processes which can affect such characteristics as body size, sexual maturity, and intensity of skin pigmentation. In Figure 1.6, this fact is represented by the presence of several arrows pointing toward each one of the characters represented at the right-hand side of the diagram. Conversely many differences controlled by single genes affect a large number of different characteristics of the adult organism. This is because a disturbance or a change in the rate of some basic metabolic or synthetic process, such as the formation of cartilage or bone in a higher animal or of lignified cell walls in a higher plant, is bound to affect many different organs in various ways. In many instances, particularly in the case of the synthesis of enzymes and other basic processes of cellular metabolism, a gene-controlled difference can have a "feedback" effect on the rate of duplication or activity of the genes themselves. Such feedbacks are represented in Figure 1.6 by arrows pointing from right to left. Figure 1.7 supplements Figure

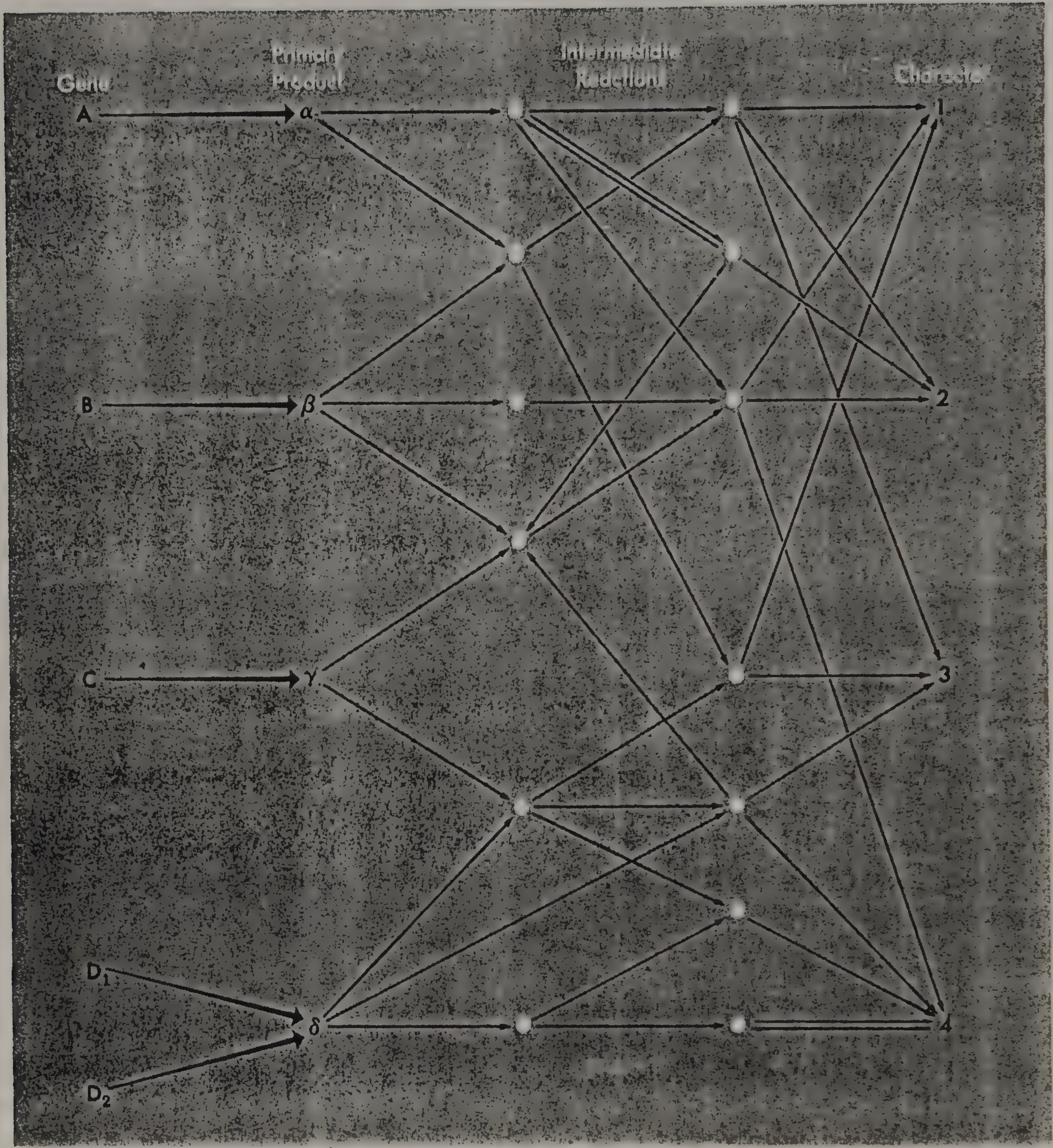


Fig. 1.6 Diagram showing the complex interrelationships between genes and characters which result from the existence of genes with multiple or pleiotropic end effects, from the multiple factor basis of inheritance of most adult characteristics, and from the frequent presence of "feedback" interactions by which intermediate products of the action of one gene can affect primary products of another gene.

1.6 with a representation of specific metabolic processes which must take place in a higher organism between the initial activity of genes and the final expression of morphological characteristics. No effort has been made to exaggerate complexity in making this diagram; if anything it is an oversimplification of the network of processes which actually takes place.

Fig. 1.7 Diagram showing some of the metabolic processes which intervene between the primary action of genes and the final expression of characters in a higher organism.

This developmental complexity is important to students of evolution for the following reason. Natural selection acts at all stages of development, but much of its action is on the final characteristics of the adult organism. Evolutionary change, however, depends on alterations of the frequency of particulate genes in the population. The complexity of the pattern of developmental processes illustrated in Figures 1.6 and 1.7 is a measure of the degree of indirectness of the effects of natural selection on evolution. Because a single visible difference is usually controlled by many genes, any action of selection which affects this difference will automatically alter the frequency of several different genes in the population. Conversely, if the frequency of a gene is altered by the selective advantage or disadvantage of one of its end effects, several other characteristics over which it also exerts partial control will be simultaneously altered. Before biologists can understand fully the ways in which selection can produce visible differences between races and species, they must explore more deeply into a great *terra incognita* of modern biology; the complex network of pathways between genes and characters.

The resolution of these complex difficulties, and the synthesis of a coherent theory of evolution which takes into account all of the pertinent facts of modern biology, has been the work of several biologists during the past thirty years. The first edition of Dobzhansky's now classic book, *Genetics and the Origin of Species*, which appeared in 1937, set the stage, and stimulated biologists in several fields to contribute to the synthesis. Books by zoologists Julian Huxley and Ernst Mayr showed how the modern theory could explain the origin of variation patterns in higher animals, and the present writer attempted to do the same for higher plants. A leading paleontologist, George Simpson, showed in two books that the fossil record of higher animals is best explained by assuming that throughout the evolutionary history of living things those same processes took place which were being experimentally demonstrated by many workers in populations of contemporary animals. He, Bernhard Rensch, and others have made a strong case for the belief that the evolution of genera, families, and higher categories of animals has taken place through an extension into long periods of time of those same processes which at any one time level govern the origin of races and species.

Chapter Summary

Modern biologists accept evolution as a fact, as well-documented as the known facts of ancient history. They base this conclusion chiefly upon quantitative experiments and observations of evolutionary processes that can be observed taking place in contemporary populations of animals and plants. These scientific data are reinforced by extrapolations to past events, based partly upon knowledge of the fossil record, and partly upon comparative studies of contemporary organisms. Evolution is the cornerstone for the explanation of

the diversity of living organisms. The basic processes of evolution are five: (1) Mutation and (2) genetic recombination are the sources of variability, but do not provide direction. They contribute variability to a gene pool represented by the variant individuals composing any cross fertilizing population in nature. (3) Chromosomal organization and its variation, which affect genetic linkage, produce orderly arrangements of variation in the gene pool, which changes its composition through the guidance of (4) natural selection. Limits to the direction in which selection can guide the population are set by (5) reproductive isolation.

Charles Darwin in his book, *The Origin of Species*, provided evidence which convinced most biologists that evolution has occurred and produced the theory of natural selection to explain it. The weakness in his theory, ignorance of the nature of heredity, was removed when, in the 1920's and 1930's, Mendelian principles of inheritance were correctly applied to populations and used to explain genetic variability in nature. A conflict which existed in the first quarter of the twentieth century between Darwinian naturalists and early Mendelian geneticists was resolved by this research in population genetics. The modern synthetic theory of evolutionary processes, which is the theme of this book, is the result.

Questions for Thought and Discussion

1. What have been the roles of observation, experiment, and extrapolation in establishing the validity of evolutionary theory?

2. What characteristics of Darwin's work and of the period in which he lived contributed the most to the favorable reception which his theory received, as compared to Lamarck and others of Darwin's predecessors?

3. Do you think that Darwin would have radically changed the last edition of *The Origin of Species* (published in 1872) if he had known about Mendel's discoveries when they were made (1865)? Give reasons for your answer.

4. What are the similarities and differences between Darwinian and modern concepts of evolutionary processes? In what ways has Mendelian genetics contributed toward establishing these differences?

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